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A quarterly paper devoted to the sugar interests of Hawaii and issued by the Experiment Station for circulation among the plantations of the Hawaiian Sugar Planters' Association.

In This Issue:

A Giant Macadamia Nut:

A species of macadamia nut, over twice the size of the varieties now growing in Hawaii, was discovered in the forests of North Queensland in 1889. Plans for its importation into Hawaii are now underway by the Botany and Forestry Department. A single tree was located in August 1935, near the point of original discovery, from which it is hoped viable seed may be obtained. A recent expedition in search of it is described, together with facts pertaining to its history, usefulness and normal habitat.

A Preliminary Report on an Entomological Survey of Guam:

Transpacific airplane service opens a new gate for the entrance of foreign insect pests to our Territory. The island of Guam is the most important and largest stopping place for planes plying between the Philippines and Hawaii and a stepping stone for oriental pests eastward. An entomological survey of that Island by O. H. Swezey is placing on record vital information of great value in the formulation of quarantine procedures for Hawaii and incidentally for the mainland of the United States.

Comparative Hardness of Tasseled versus Untasseled Canes:

In 4500 tests comparing the rind hardness of tasseled versus untasseled canes all of the same age and growing in close proximity, the former are shown to be consistently softer. These comparative studies were made possible in the field through the use of an instrument specially designed for the purpose. This is described and illustrated. The bearing of this investigation on beetle borer infestations is discussed.

Soil Reaction and Total Acidity:

The meaning and significance of such terms as reaction, pH, total acidity and buffers are discussed, with special reference to Hawaiian soils. The processes by which Hawaiian soils have been formed and have become acid or alkaline are de-

scribed. The effects of various agricultural practices upon soil reaction and total acidity and measures to prevent undesirable effects due to excessive acidity or alkalinity are outlined.

The Fluctuations of Sugars in the Leaf Sheaths of the Sugar Cane Plant During the Day and the Night:

Problems concerning the movement of sugar from the blade to the stem of the sugar cane plant are presented, the discussion being based upon analyses of sheaths taken at hourly intervals during the day and the night. The results indicate that the transport of sugar occurs both day and night, that both cane sugar and simple sugars are translocated, and that the factors affecting the movement of sugar include the amount of water and interchanges with other compounds.

Further Notes on Water and Cane Ripening:

This is the second in a series of studies designed to determine what effects the withholding or supplying of water will have upon the formation and storage of sugar in the cane plant. The results indicate that the plants receiving water were superior in the manufacture of sugar in the leaves and in its transport to the stems, whereas the plants deprived of water were superior in the storage or conservation of sugar in the stems. Although the plants deprived of water had the higher percentages of cane sugar in the tissue of the stem, the plants receiving water yielded, in general, the better juices, indicating that the sugar present in the plants receiving water was more readily expressed than that in the plants deprived of water.

A Giant Macadamia Nut

By C. E. Pemberton

In 1889, F. Manson Bailey, Colonial Botanist of Queensland, Australia, while engaged in a botanical exploration of the dense tropical forests of the cloud-enshrouded Bellenden Ker Range in North Queensland, which composes the highest mountains of that state, discovered a new species of macadamia nut, the fruit of which measured over two inches in diameter. In a comprehensive botanical publication (*The Queensland Flora,* part 4, page 1330. 1901), appears Bailey's description of this particular tree, under the name *Macadamia Whelani* Bail., together with the statement that it was "Abundant along Tringilburra Creek, and thence to Whelanian Pools," and further that "The nuts seem to be largely used by the natives of this locality for food, as we found large quantities of the broken shells as well as the whole nuts at all their camps." Beyond these original observations by Bailey and his final, brief discussion of it in the above monograph in the terse, technical language of the thorough taxonomist, apparently no further notice was given to the existence of this interesting tree until Dr. H. L. Lyon gave it consideration as a species desirable for study and introduction to Hawaii.

During May 1935, R. W. Mungomery, Chief Entomologist for the Queensland Bureau of Sugar Experiment Stations, spent some weeks visiting at the Experiment Station of the H. S. P. A. and when questioned by Dr. Lyon as to the location of Tringilburra Creek, above mentioned, indicated its position on the map. Later in the year when the writer was in Queensland near the Bellender Ker mountain range with Mr. Mungomery, the creek was pointed out where it could be seen descending from a densely forested mountain region into the valley below. Decision was immediately made to penetrate the range up this creek in an effort to re-discover this large-fruited macadamia nut. The exit of this creek into the lowlands was found to be so choked with high, impenetrable thickets of lantana, greatly exceeding those which may be found anywhere in Hawaii today, that Fishery Falls Creek, some 5 miles away, which led out from the same mountain range, was selected for examination because more easily approached and provided with a well-cut trail. This creek lies some 24 miles from Cairns, North Queensland and tumbles directly out of the dark Bellenden Ker Range as a cool, clear stream of fair volume.

On September 18, 1935, the writer, accompanied by J. H. Buzacott, Assistant Entomologist, Queensland Bureau of Sugar Experiment Stations, visited Fishery Falls Creek in search of the tree in question. After following the creek bed and carefully examining the trees for an hour or more, until the fine, thick forest, which completely clothes the mountain, had been well entered and the stream bed had become steep and more difficult of passage, a halt was made in the deep shade among huge boulders and a rushing torrent. No signs of the coveted tree had been seen and it was feared the search was in vain, when a single, very large and completely hollowed out macadamia nut, half eaten by rats, was discovered lodged in a crevice between some large boulders. By radiating from this spot and carefully searching amongst the leaf mould and rocks near the stream, several more nuts in a similar

condition were picked up. Ultimately a fine large macadamia tree was found some two feet in diameter near the base, with a smooth, straight trunk extending up 40 feet or more to the first large branch, and with the topmost branches reaching into the sunlight 60 to 70 feet above the floor of the forest. High overhead amongst the upper foliage some branches could be seen bearing a number of apparently ripe nuts and beneath the tree many could be found that had been partially destroyed by rats.

On the following day the party returned to the spot accompanied by G. L. Windred, Chief Entomologist of the Colonial Sugar Refining Company of Australia, who is shown on the cover page of this issue holding a fruiting branch of *Macadamia Whelani*. Ascent of the tree was a difficulty surmounted by Mr. Buzacott, who succeeded in climbing the slippery trunk with the aid of climbing irons attached to his feet, and after much labor obtained most of the fruits on the tree, comprising about 100 in all. These were carefully dried and brought by the writer to Honolulu on October 28, 1935. They were planted under Dr. Lyon's supervision but failed to germinate, which suggests that they were still too immature for removal from the tree when collected, or that the method of transportation was wrong. Further attempts to secure better seed are underway, utilizing again the generous assistance of Messrs. Mungomery and Buzacott, whose help and that of Mr. Windred are hereby gratefully acknowledged.

This tree is of special interest owing to the large size of the nuts. It is rather surprising that attempts to commercialize the species have not been made in view of the findings of Bailey in 1889, who obtained fairly reliable evidence that the nut was edible and in considerable use amongst the natives. In the present instance none of the fruits were eaten. The number collected was so small that all were saved for planting. The shell is very hard and somewhat thicker than that of the common commercially planted macadamia nut, but this nut will probably contain twice as much meat as the smaller species, or perhaps more. It is also interesting to speculate on the possibilities arising from hybridization of the two species.

The accompanying photographs will serve to illustrate the tree from which the nuts were collected, the size of the fruit, and the general complex of vegetation, all striving for existence in the tangled jungle where the tree was found.

Fig. 1. The lower portion of the trunk of *Macadamia Whelani* Bail. Diameter about 1½ to 2 feet.

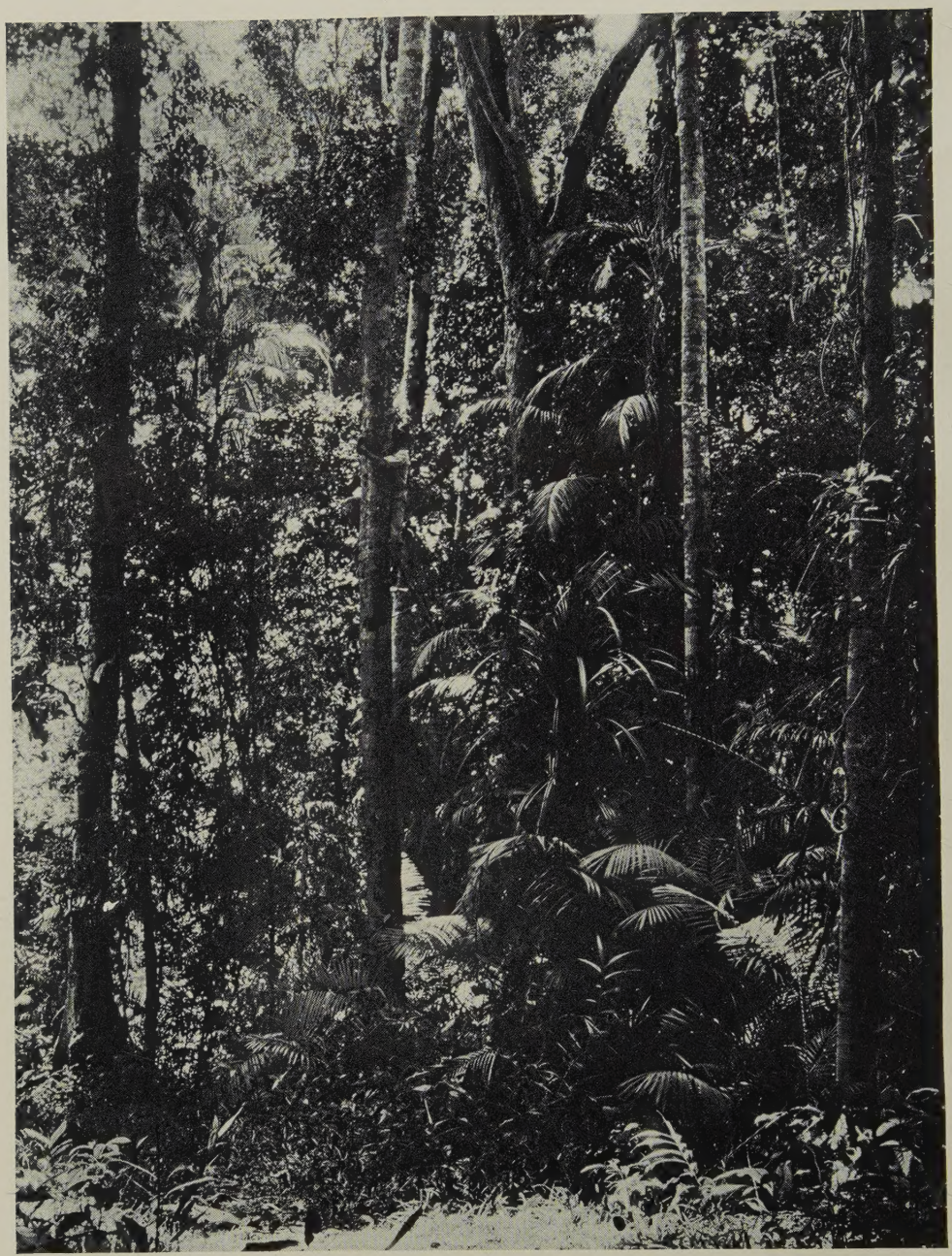

Fig. 2. Showing a well grown specimen of *Macadamia Whelani* Bail. at left center, in a typical North Queensland tropical forest. The figure of a man can be seen climbing the tree half way up the trunk, which will indicate the proportions of the tree.

A Preliminary Report on an Entomological Survey of Guam*

By O. H. Swezey

We arrived in Guam on April 27, 1936, and commenced the survey as soon as possible after getting settled in a residence, provided by the Governor, on the grounds of the Edmund S. Root Agricultural School at Piti, 4½ miles southwest of Agana, the Capital city. An endeavor has been made to ascertain all the insects connected with each of the various crops. The small farms, or ranches (no matter how small, they are called ranches, and a few are as extensive as two or three thousand acres, much of which is wild land) are scattered over all parts of the Island. In some regions the land is fully occupied agriculturally, but many ranches are in clearings in the midst of dense tropical jungle. Many of the ranches have been visited in various sections in order to make observations on the insects associated with the various crops. Those situated in the clearings in the jungle have made a convenient access to the native trees, and much knowledge has also been gained of the insect faunas of the more important trees. The crop pests, that is, those known at the present time, are listed as follows, names being used when known, but some are as yet without names:

Coconut

The coconut is the only crop being produced for export; 1809 tons of copra being exported last year. Coconut trees are everywhere from one end of the Island to the other. Most of them have been planted, but some are volunteers. Much of the corn and vegetable crops are grown beneath or among the coconut trees. At present, coconut trees are not severely injured by insects, but the following attack them to some extent:

Aspidiotus destructor is the notorious coconut scale which so nearly ruined the coconut trees of Saipan some years ago. It never became so serious on Guam, as it has been controlled by a tiny black ladybeetle *(Cryptogonus nigripennis)* and a few chalcid parasites, the ladybeetle being the most important. At present, only an occasional small colony of the scale is to be found on the coconut leaves. It is likewise occasionally found on banana leaves, and I have also found it on avocado, mango, grape, rose, and jasmine.

Pseudococcus cocotis is a mealybug found to some slight extent on coconut trees.

Phasmids: One or possibly two species of stick insects sometimes feed extensively on the leaves, giving them a somewhat ragged appearance.

Tineid: The larvae of a small moth feed on the under side of leaves, singly, and produce short, narrow, dead streaks where they eat off the under part of the leaf. From the present appearance of the leaves, these larvae must have been very numerous at some time, but during the months I have been here, they have been very scarce.

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* Printed with the kind consent of Governor B. V. McCandlish of Guam, under whose jurisdiction this survey is being conducted.

Rhabdocnemis obscura and *Diocalendra taitense:* The larvae of these two weevils feed to some extent in the stubs of cut off leaves. Once an old cocoon of *obscura* was found in the husk of a coconut where the larva had fed.

Necrobia rufipes is of course present, as it is always on copra.

Scholastes bimaculatus: The maggots of this fly feed in decaying coconuts; it is not common.

Corn

Corn is the next crop of importance. It is grown by all the ranchers, and is largely used for human food, both green and when ripe. Two to three crops are grown annually, and it is found in all stages of growth at all times. Its pests are as follows:

Pyrausta nubilalis, the European corn borer, once a pest reported as taking half of the corn crop, is now satisfactorily controlled by a tachinid fly *(Ceromasia lepida)* introduced from Japan in 1931. In the mainland of United States this corn borer feeds on many kinds of plants, but in Guam, I have found it only on corn.

Chloridea obsoleta: The corn earworm is the most injurious pest. About 2 per cent or more of the ears are attacked by it, and sometimes the percentage is higher, but I have not found it to be nearly the pest that it is in Hawaii during recent years.

Marasmia trapezalis: The corn leafroller is nearly always present on young corn plants, the caterpillars rolling the tip portion of the leaf for protection. If growing conditions are favorable, the plant is not appreciably checked by the leaf-rollers. These leafrollers are less common as the plant becomes older; some are parasitized by a braconid wasp *(Apanteles* sp.).

Agromyzid: A tiny black fly the larvae of which feed very abundantly in the leaves of young corn plants. They produce narrow mines running longitudinally, often as many as one hundred per leaf. They are most numerous in the apical half of the leaf, causing early drying up and dying of the leaf. The succeeding new leaves are attacked less, perhaps on account of an Eulophid parasite which works in fair numbers on the leafminer maggots.

Prodenia litura: Caterpillars of this noctuid moth have occasionally been found feeding on corn leaves.

Peregrinus maidis: The corn leafhopper is usually to be found, but not in serious infestations. It is attended by a small green bug *(Cyrtorhinus lividipennis)* which apparently has the same relation to it that *Cyrtorhinus mundulus* has to the cane leafhopper in Hawaii.

Aphis maidis often causes bad infestations of the tassels when they are about to expand. A large ladybeetle *(Harmonia arcuata)* is especially abundant and with one or two others quickly reduce these infestations. The syrphid fly *Simosyrphus grandicornis* is also common, its maggots feeding on the aphids.

Grasshoppers: Two or three species of grasshoppers feed on corn leaves to some extent.

Calendra oryzae: The rice weevil is injurious to stored corn. Often a great deal of corn is destroyed when not properly stored, or not properly treated to kill the weevils.

Rice

Rice is an important crop, being grown in the river valleys where the land is favorably located for irrigation. Only one crop is grown per year, it being planted in September during the rainy season. It ripens for harvesting during the succeeding dry season. Not enough is grown for local consumption, and a considerable amount is imported from Japan. A large number of insects are found in rice fields, some of them causing considerable loss.

Leptocorisa sp: The rice bug is a large insect; it punctures and feeds on the soft growing rice kernels.

Mirids: Two species of leaf bugs.

Cicadellids: Two species of leafhoppers.

Delphacid leafhopper: It is parasitized to a considerable extent by a dryinid.

Grasshoppers: Three or four species, one of which feeds largely on the heads of the rice when the kernels are still soft.

Leafroller: The leaves are often eaten by a small caterpillar which rolls the leaf for protection, yet is well parasitized by a braconid (*Apanteles* sp.).

Tineid: A tiny moth larva is sometimes found in the rice heads.

Pyralid moth: The larvae were found feeding among decaying leaves at the base of rice stools. It is not certain whether or not they sometimes feed on the growing plant.

Armyworms are said to cause considerable damage in the seedling plots, but I have not as yet seen any.

Sugar Cane

Sugar cane is of little importance at the present time, less of it being grown than in former times. There are patches of not more than two to three acres, and little attention is given to it. The juice is extracted by crude vertical wooden rollers operated by a sweep drawn by a carabao. Boiling is done in large, open, iron kettles fixed in a concrete furnace. The resulting molasses is either used at a local distillery, or made into peanut candy for local consumption. There is a tendency toward a revival of cane growing with the distribution of seed from the Root Agricultural School farm where several varieties were received from Honolulu early in 1935; this seed is distributed at each time of cutting. The cane insects are for the most part the same species as those in Hawaii.

Rhabdocnemis obscura: The cane borer is not very injurious where the patches of cane are well taken care of, but in neglected patches it does considerable damage. At one time the tachinid fly *Ceromasia sphenophori* was established by colonies from Honolulu, but it has entirely disappeared.

Perkinsiella thompsoni: A leafhopper closely related to the cane leafhopper in Hawaii. It is very scarce, and its eggs when found are mostly parasitized by a species of *Paranagrus*.

Trionymus sacchari: The pink mealybug is often to be found but is not of much importance. A fungus disease seems to control it rather well.

Pseudococcus boninsis: The gray mealybug is also occasionally found. A parasite was reared from it which seems to be *Aphycus terryi* which is also present in Hawaii.

Pseudococcus brevipes: The pineapple mealybug is also occasionally found on cane.

Aphis sacchari and the stalk mite: I have not seen these on cane in Guam.

Grasshopper: A large species, which is generally prevalent, sometimes feeds on cane and causes a few ragged leaves.

Cane Rust was found in a few cane patches. This is a disease not yet known in Hawaii. Some other peculiar spottings of leaves have been observed, and preserved specimens have been sent to the Experiment Station for study; typical lesions of brown stripe and leaf freckle were found on certain leaves while two unknown leaf markings were observed on other leaves.

Taro

Taro is grown everywhere—the upland varieties. I have not found it damaged by insects, although the following are sometimes present:

Prodenia litura: Eggs of this noctuid moth are deposited in clusters on the under side of the leaf. The young larvae eat gregariously for a while then scatter to nibble here and there. Most of them disappear before maturity. I think that probably the yellow-jacket wasps prey on them. This and two other wasps are very abundant and always on the search for caterpillars; they are undoubtedly of great importance in the control of this moth, other caterpillars, and the numerous kinds of leafrollers.

Megamelus proserpina: The taro leafhopper is sometimes found, but not abundant enough for noticeable injury.

Aphis gossypii: The cotton aphis is sometimes found slightly infesting taro leaves. It is parasitized by a species of *Aphelinus* and preyed upon by syrphid larvae.

Aleyrodid: In one taro patch an aleyrodid was found on some of the leaves.

Tobacco

Tobacco is grown only in occasional small patches.

Chloridea obsoleta: Caterpillars of the corn earworm spoil many of the leaves unless handpicking is resorted to.

Prodenia litura: Caterpillars of this noctuid moth feed on tobacco to a slight extent.

Grasshoppers: Two or three species damage the leaves to some extent.

Mirid bug: A small species is common on tobacco.

Banana

The banana is another plant which is grown very generally, but in a scattered way—not in mass formation. A few species of insects attack it.

Aspidiotus destructor: The coconut scale is occasionally found in small colonies on the leaves, a yellowish area indicating the presence of the colony.

Prodenia litura: Caterpillars of this moth do more conspicuous damage to the leaves. The freshly hatched caterpillars feed near where the eggs were located, but

soon scatter, nibbling here and there on the under surface of the leaf. When larger they feed along the midrib thus injuring the leaf so that it soon becomes brown and dead.

Scarabeid: A large brown beetle which at times feeds extensively on banana leaves at night time, remaining hidden during the day.

Grasshopper: A large grasshopper sometimes feeds on banana leaves.

Cosmopolites sordidus: The widely spread banana borer is present. The adult weevils are always to be found in the base of old decaying banana plants, and the larvae are found in growing stems as well.

Polytes mellerborgi: A smaller weevil often found under similar conditions to the banana borer, the larvae feeding chiefly in the base or corm of the plant.

Orange

Several kinds of citrus fruits are grown, and the same kinds of insects affect all of them.

Papilio xuthus: This swallowtail butterfly is very common. Its caterpillars feed on citrus foliage.

Leafminer: The larvae of a minute moth mine the newly growing leaves causing them to be very much crumpled and deformed, and eventually to die prematurely.

Icerya purchasi: The cottony cushion scale is well controlled by *Novius cardinalis,* introduced from Hawaii in 1926.

Scales: Two or three species are sometimes found.

Gummosis: A disease of the bark which is more destructive than the insect pests. Wood-boring beetles attack the trees which are dying from gummosis.

I have not found fruit flies in citrus or any other cultivated fruits, but a pretty species was reared from a native fruit *(Ochrosia* sp.), and was found to be highly parasitized by a braconid *(Opius* sp.).

Pineapple

The pineapple is not grown extensively. The only insect pest so far noted on it is the mealybug *Pseudococcus brevipes.* It is usually scarce, but an occasional fruit is seen with a considerable infestation. Apparently it is well controlled by a small black ladybeetle with a reddish spot towards the apex of each elytron. It seems to be a species, near *Scymnus bipunctatus,* present in Hawaii. This ladybeetle works on *Ferrisia virgata* and other mealybugs. *Cryptolaemus montrouzieri* is also very common and helps greatly to control the mealybugs.

Mango

Mango trees are sometimes nearly defoliated by a chrysomelid beetle *(Phytorus pinguis).* These beetles also feed on many other kinds of trees. They seem to be seasonal, occurring mostly in the dry season. A few scales are also found on mango: *Ceroplastes floridensis, Lepidosaphes* sp., *Aspidiotus destructor,* and the thread scale.

Beans

Several kinds of beans are grown generally, and attacked by the following:

Leafroller: The larvae of an undetermined pyralid moth feed on the leaves to some extent.

Archips rosaceana: The larvae of this tortricid leafroller occasionally feed on bean leaves. It is a general pest, occurring on many plants. I have reared it from the leaves of 19 kinds of trees and plants, some of them being native trees. It is an immigrant insect first reported in 1926.

Tortricid: The larvae of another tortricid moth are often found in bean pods, eating the seeds both of pole beans and lima beans. It is a moth very much like the moth the larvae of which destroy Koa seeds and also feed in the pods of *Acacia farnesiana* and some other legumes in Hawaii. The larvae destroy a large proportion of the seeds of *Pithecolobium dulce* and *Adenanthera pavonina* here in Guam. I made a count in 29 pods of the latter and 77 per cent of the seeds were found destroyed.

Cabbage

At least three kinds of caterpillars feed on cabbages and related vegetables: *Prodenia litura, Hellula undalis,* and an undetermined species. The second one named is the most destructive. The cabbage butterfly is not found in Guam.

Miscellaneous Vegetables

Each kind of vegetable grown has one or more particular pests which will not be enumerated in this preliminary report.

Forest Insects

Besides the leafminers and leafrollers already mentioned, I have reared a large number of species of insects from the various native forest trees, and other caterpillars have also been reared, producing a large assemblage of moths which have never been known or reported from Guam. Probably all of these when studied will be found to be new species. Each is particularly associated with its own special food plant. A great deal of material in the other Orders of insects has also been obtained.

Crop Pests in Guam Which Do Not Occur in Hawaii

Coconut: *Aspidiotus destructor.* Coconut scale.
Pseudococcus cocotis. Mealybug.
Phasmid. Stick insect.
Tineid moth.

Corn: *Pyrausta nubilalis.* European corn borer.
Marasmia trapezalis. Leafroller.
Agromyzid. Leafminer.

Rice: *Leptocorisa* sp. Rice bug.
Mirid. Leaf bug.
Cicadellid leafhoppers. Two species.
Delphacid leafhopper.
Grasshoppers. Three or four species.
Leafroller. Pyralid moth.
Tineid moth. Larvae in heads.

Cane: *Perkinsiella thompsoni.* Leafhopper.
Cane rust. Disease of the leaves.

Taro: *Prodenia litura.* Noctuid moth.
Aleyrodid.
Megamelus proserpina. Leafhopper.
(I recently learned that this has appeared in Honolulu.)

Tobacco: *Prodenia litura.*
Mirid bug.
Grasshoppers.

Banana: *Prodenia litura.*
Aspidiotus destructor. Coconut scale.
Scarabeid. Large brown beetle.
Cosmopolites sordidus. Weevil borer.

Orange: *Papilio xuthus.* Swallowtail butterfly.
Leafminer. Minute moth.
Gummosis. A bad bark disease.

Mango: *Phytorus pinguis.* Chrysomelid beetle.
Ceroplastes floridensis. Wax scale.

Beans: Leafminer. Small moth.
Archips rosaceana. Tortricid leafroller.
Pyralid leafroller.
Tortricid. Larva in pods.

There are over 30, and about a dozen of them not previously reported from Guam.

Mosquitoes

Two kinds of mosquitoes occur in Guam:

Culex quinquefasciata the common night mosquito, which is found breeding in water barrels (gasoline drums), tin cans, pools, hog wallows, etc.

Aedes sp. A day mosquito which has not been positively determined yet. It inhabits for the most part the wild lands and forests, where it continually annoys the visitor to those regions. Its bite is not so severe as the bite of the day mosquito in Hawaii. The only place in which I have found their larvae is in the accumulated water at the axils of *Pandanus* leaves. *Pandanus* trees are numerous in the forests, two or three species, and even in dry weather I found that they contained water and mosquito wrigglers.

House Fly

House flies are very abundant about houses, and also out in the forests, in fact everywhere. Generally they seem to be a smaller species than the usual house fly. They breed abundantly in cow dung and carabao dung of which there is an abundance for the purpose. Several other flies breed in the same material.

Acknowledgment

Our work has been facilitated by members of the Governor's office, the Department of Agriculture, and the Edmund S. Root Agricultural School, who have cooperated in rendering assistance in meeting ranchers of the various districts, and in visiting desirable outlying locations in extreme parts of the Island. Captain Stephenson of the Marine Corps supplied us with large-scale contour maps which have been indispensable.

Comparative Hardness of Tasseled Versus Untasseled Canes

By C. E. Pemberton

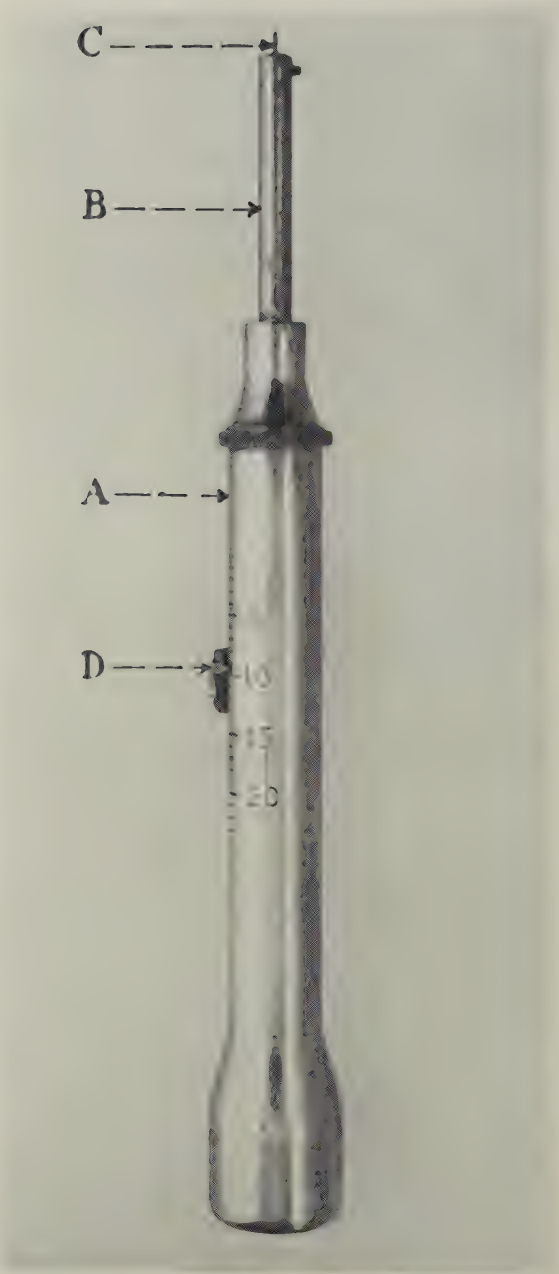
Soft canes are usually considered susceptible to attack by the beetle borer *Rhabdocnemis obscura* Boisd., while hard varieties are generally believed to be resistant or but slightly damaged by this insect. Actual field experience supports these views. Just why a soft cane offers greater susceptibility than a hard one is problematical, since soft, tender, stalk tissue beneath a live leaf sheath is always accessible to the egg-laying female in even the hardest of canes and is the normal place for the beetle to insert its eggs. The fact, however, that soft canes are more frequently damaged by the beetle borer than hard ones, is so well established that systematic measurements are being made, with special instruments constructed for the purpose, of the hardness of many of the promising seedlings recently produced at this Experiment Station, in the belief that these data will indicate to a certain extent the degree of borer susceptibility to be manifested by each variety when spread on plantations where the borer is prevalent.

A large number of these measurements were made during March and April, 1936. All of the canes had passed through the tasseling season of 1935 and many had tasseled. The tests were made with a new instrument (see accompanying illustration), designed by Dr. H. L. Lyon, which permits field, rather than laboratory study. This instrument is quite similar to one used in India, which was described and illustrated in "Agriculture and Live-stock in India," March 1935, pages 156-158. This greatly facilitated a better interpretation of the data, since the specific environment and growth condition of particular stalks, exhibiting wide variations from the normal of the variety being tested, could be examined on the ground at the time the measurements were being made. In the course of this work, an apparently wide error or variation in the hardness of certain stalks in any given variety was frequently encountered. It soon became obvious that these large deviations from the normal occurred in canes which had tasseled. They were invariably softer than the untasseled canes of approximately the same age, even when both were part of the same stool. This led to a particular study of the relative hardness of tasseled versus untasseled canes in 9 varieties which had tasseled considerably during the latter part of 1935. The varieties selected were chosen at random, with no previous knowledge of their rind characteristics. The results are tabulated below:

TABLE I

Comparative Hardness of Tasseled Versus Untasseled Canes

	Tasseled		Untasseled		
Variety	No. Tests	Hardness	No. Tests	Hardness	Ratio
POJ 2878	250	4.9	250	10.6	2.16
31-3040	250	7.5	250	14.5	1.93
32-177	250	7.9	250	13.9	1.76
31-3012	250	6.2	250	12.3	1.98
29-2196	250	6.9	250	15.1	2.18
32-1577	250	6.9	250	16.3	2.36
32-1594	250	8.7	250	17.0	1.95
32-1756	250	5.9	250	10.3	1.74
27-8101	250	3.9	250	8.4	2.15



Instrument for measuring the comparative hardness of various canes. Consists of hollow cylinder "A," containing spring attached to plunger "B," which bears removable needle-point "C." Pressure of the point against the cane rind compresses the spring and causes the pointer "D" to slide along the indicator scale and register the number of units of pressure required to force the point into the rind. Reduced one half.

In all of the above tests, both tasseled and untasseled canes were growing in the same field and were approximately the same age. All records were taken in the bottom 4 or 5 joints. No readings were recorded for canes which had tasseled and failed to *lala,* since these stalks were either dead or in the rapid process of dying. Such canes are always very soft.

It will be noted that in 7 out of the 9 varieties selected for study, the untasseled stalks were nearly 2 to 2½ times as hard as those which had tasseled, and in the remaining two cases the untasseled canes were also much harder than those which had arrowed.

During these investigations it soon became evident that stalks in any given variety which *lala* profusely after tasseling, are not as soft as those of the same variety which *lala* very weakly. The process of dying or disintegration after flowering becomes greatly suspended in all parts of the stalk if side shoots are vigorous. This is revealed in the rind studies and can be expressed to some extent in terms of rind hardness, when comparisons are made with untasseled stalks of the same variety, the same age, and from the same part of the field.

The fact that canes which have tasseled are definitely softer than those which have not, may explain the greater incidence of beetle borer infestation in some areas in Hawaii where certain varieties tassel very heavily. Kahuku Plantation Company is a good example to illustrate this point. There tasseling is usually considered excessive with some varieties and beetle borer infestation is often conspicuous. This is particularly to be expected if rainy and windy weather has prevailed after the tasseling season.

Soil Reaction and Total Acidity

(A Discussion of Soil pH, Base Exchange and Kindred Topics—
Terms of Everyday Usage)

By Francis E. Hance and L. E. Davis

The agricultural importance of "sour" or acid soils has been recognized for a very long time. It was known three thousand years ago that some infertile soils could be improved by liming (16)*. During the last century the attention of agriculturists was directed more and more toward means for measuring the acidity or alkalinity of soils and correcting adverse soil conditions resulting from excesses of either.

Soil acidity has two quite different aspects which are commonly known as soil reaction and total acidity. The former has been given a great deal of attention by soil chemists who have devised numerous methods and types of apparatus to measure it. Total acidity has been studied somewhat less intensively perhaps; at least routine laboratories usually determine soil reaction more frequently than total acidity.

Acids and Bases (23)

Before we consider soil acidity it may be desirable to discuss as briefly as possible the meaning of the terms "acid" and "base," as they are used in chemistry. Everyone is familiar in daily life with acids and alkaline substances. Strong *acids* are substances which taste sour, such as the muriatic acid of industry or the citric acid of lemons. They corrode certain metals such as iron and zinc, forming salts of these metals and causing evolution of an inflammable gas—hydrogen. All acids, when in solution in water, yield free hydrogen ions. The chemist classifies as acids many substances which neither taste appreciably sour nor corrode metals, such as the druggists' boracic acid, the soap makers' stearic acid, etc.

Another group of substances commonly known as lyes, caustics, etc., and exemplified by soda lye, borax and ammonia water, is given the name *bases* by chemists. These compounds, when strongly active, combine with fats to produce soaps and are very caustic or corrosive. When a drop of a solution of caustic soda is rubbed between the fingers a sensation of slipperiness is observed which persists to some extent even after washing with water. The weaker members of this family also grade down in intensity of these properties to substances which do not perceptibly exhibit these characteristics. Acids are generally said to have acid or acidic properties; bases, alkaline or basic properties.

Either strongly acid or alkaline substances, when sufficiently concentrated, attack the tissues of plants and animals and are dangerous poisons when taken internally.

*Numbers in parentheses refer to literature cited. A number of text and reference books dealing with broad phases of the subjects discussed in this paper are included. References to these books may be found immediately after the various sub-titles.

The antidote for an acid is a base, and vice-versa. These two classes of compounds have the property of mutually destroying the primary characteristics of each other. They *neutralize* one another. We thus arrive at a simple and inclusive definition of acids and bases: Strong acids (or bases) may be defined in terms of their most obvious properties; sourness, etc. in the case of acids, or ability to combine with fats to produce soaps, etc. in the case of alkalies; bases (weak or strong) are compounds which neutralize acids; acids (weak or strong) neutralize bases.

Total Acidity of Soils (4, 10, 18)

Soils are exceedingly complex mixtures of many different materials, including fragments of the original rocks from which the soil was formed, mineral constituents formed from the original rocks by weathering, and organic matter produced by the partial decomposition of plant and animal residues. The last two classes are composed of chemically active substances which constitute the seat of the more rapid changes taking place in the soil. These substances may display acid or alkaline characteristics, and the soil is then described as acid or alkaline. The degree of acidity or alkalinity is usually low. Even the most acid soils are by comparison with such substances as vinegar and lemon juice actually only weakly acidified so that an acid soil rarely has a sour taste and does not corrode metals because of its acid constituents alone. However, soils will neutralize and be neutralized by acids or bases if they are alkaline or acidic, respectively. A given quantity of an acid (whether in a solution, soil, or other material) is always exactly neutralized by some definite quantity of an alkaline compound. The amount of the latter required is then a measure of the amount of acid present. This quantity is called the *total acidity*, or (because the determination of its value is frequently made by an analytical procedure called titration) the titratable acidity.

As previously stated, when certain metals are attacked by strong acids the gas hydrogen is evolved. It has been established that all solutions of acids contain hydrogen. The distinctive properties of acids are due to hydrogen, although hydrogen in combination with other elements does not always produce acidity. The loss of hydrogen as a gas causes the acidic properties to decrease in intensity and the metals are therefore called bases. Alkaline substances contain metals or certain groups of chemical elements (such as ammonium, a group composed of nitrogen and hydrogen) which play the same rôle as the metals. These metals or allied groups are also called bases.

The acidic properties of soils are due to hydrogen present as a constituent of compounds in the soil. Metallic or other bases are also found in the soil. The acidity or alkalinity of a soil depends upon the relation between the amounts of soil hydrogen and soil bases.

When soluble solid substances, such as common salt, are mixed with water they dissolve and are active chemically. Insoluble substances, such as quartz sand, do not form a solution and are not active. There are many substances which form an intermediate class, of which members of the group of minerals known as bentonites are examples. These materials do not go into true solution; nevertheless they are chemically active. Part, at least, of the hydrogen and bases in these compounds

is present in a condition of incipient solubility. Because of this activity, hydrogen or bases may be replaced by other bases or hydrogen. In the laboratory, replacement is effected by treating the material with a solution rich in the bases (or hydrogen) which are to replace those originally present (8). This phenomenon is called *base exchange* (replacement); the base-exchange (replacement) capacity is the sum of the exchangeable (replaceable) bases and the exchangeable (replaceable) hydrogen. Replaceable hydrogen is generally considered equivalent to total acidity. However, as we shall see presently, there are certain limitations upon this conception.

The chemically active portion of the soil exhibits these properties and is the seat of base exchange. It is sometimes called the base-exchange complex. Since chemical activity is not confined to the laboratory, base exchange is a process which continually operates in nature and as far as agricultural lands are concerned is affected by the addition of fertilizers and soil amendments.

Reaction and pH (2, 3, 15)

A portion of the hydrogen of an acid in solution appears to be more reactive than the remainder of the total (acid-forming) hydrogen. The direction and intensity of chemical activity is dependent upon this reactive hydrogen rather than upon the total acidity. The amount of this reactive hydrogen is called the *reaction* and may be very roughly estimated by the degree of sourness. The chemist has more precise means for measuring reaction, among which are the hydrogen electrode, glass electrode, and certain color changes of dyes called indicators.

The reaction of any acid solution depends upon the concentration of acid present and upon the strength of the acid, i.e., the relative tendency of the acid to be reactive. It is possible to have a large total acidity with a slight reaction (concentrated solutions of weak acids) or a strong reaction with a relatively low concentration of acid (dilute solutions of strong acids).

Similar considerations apply to solutions of bases where the reactive substance is a compound group or radicle called hydroxyl. We can then speak of the reaction of a base. Now, it is obvious that although solutions with strong basic reaction are quite different in properties from those of a similarly strong acid reaction, solutions of very weak acidic or basic reaction are less markedly different. It is conceivable that there may be some intermediate situation where there is neither an acid nor an alkaline reaction. Solutions exhibiting this property are said to have a *neutral* reaction or to be neutral. Since there is no essential discontinuity as we proceed from acid reactions through a neutral point to alkaline reactions, it has been found desirable to use a continuous scale of measurement and to speak of a point on this scale as simply the reaction.

Various scales have been devised. A convenient one is the pH scale which is arranged so that very highly acid reactions are assigned small values and very alkaline reactions higher numbers. The neutral point is at pH 7.0, i.e., a solution of pH 7.0 is neutral and exhibits neither an acid nor an alkaline reaction. A solution of pH 6.9 is slightly acid; one of pH 7.1 is slightly alkaline. The approximate pH values of a number of solutions are listed below:

	Approximate pH values	
Dilute solutions of strong acids	1–2	Very acid
Vinegar (5 per cent acetic acid)	2.5	
Saturated boracic acid solutions	4.5	
Sugar cane crusher juice	4.5–5.0	
Distilled water, aerated	5.5–6	
Distilled water, boiled (pure water)	7.0	Neutral
Tap water in Honolulu	7.5–8.0	
Dilute solution of baking soda	8	Very alkaline
Dilute solution of borax	9	
Lime water	10.5	
Dilute solution of washing soda	12	
Dilute solution of soda lye	13–14	

Soil Reaction (10, 18)

Soils generally range in pH from 4 to 10, with most agricultural soils falling within the narrower limits of 5 to 9. A soil with a pH of 7.0 is said to be neutral and has neither an acid nor an alkaline reaction. A neutral soil is not, however, saturated with bases to the exclusion of replaceable hydrogen. A soil can be freed from all replaceable bases by various means and is then extremely acid. If a basic substance is then gradually added to the soil the pH will increase, the replaceable hydrogen decrease, and the replaceable bases increase progressively until theoretically there is attained a quite high pH value at which all the replaceable hydrogen has been exchanged for the base. Actually, there is no practical way to reach this point because the soil is decomposed at high pH values. Accordingly, some arbitrary pH, say 7.0, must be chosen at which the process is terminated.

No particular change in the soil characteristics will necessarily take place at or near a pH of 7.0. (For a given soil there is a specific pH value, called the isoelectric point, at which changes in soil properties are quite marked. This value is rather low for most soils.) However, the habit of considering a pH of 7.0 as a unique value (induced by work with strong acids and bases) has become so fixed that most base-exchange studies are pursued with solutions at this pH. It is customary to equate the total acidity, i.e., the amount of acid neutralized to a pH of 7.0 to the replaceable hydrogen. The conventional values for replaceable hydrogen are thus less than the actual replaceable hydrogen.

Buffers (2, 3, 5)

Whenever a base is gradually added to an acid the pH increases progressively, but not necessarily at a steady rate. As an example, consider the neutralization of muriatic acid by ammonia. When the solution has been brought to a pH between 2 and 3, moderately large amounts of ammonia can be added with small changes in pH. The solution is then said to be *buffered.* It is protected against rapid fluctuations in pH. Any material having these properties is called a buffer. Buffers are very useful; they are found in nature and used in the arts and industry. By buffering a solution used in industrial processes, stability is attained. The blood is a

highly buffered medium. If it were not buffered carbonic acid produced in the tissues and acids obtained in foods would exert disastrous effects.

Although a solution of muriatic acid partially neutralized with ammonia is buffered at a pH between 2 and 3, further additions of ammonia will gradually increase the pH. As we approach a pH of 4.4 the conditions become reversed and at this point a very small addition of ammonia will cause a large change in pH. The solution now is said to be only very slightly buffered.

In general, soils are quite highly buffered throughout their normal pH range. Accordingly a soil with a pH of 6 may have a fairly high "lime requirement," i.e., a large application of lime may be required to bring the soil to a pH of 7.0. Soils are thus protected against great changes in reaction and the effect of altered conditions, particularly those due to applications of acid fertilizers, is minimized.

How Hawaiian Soils Have Become Acid or Alkaline

The original rock materials from which Hawaiian soils have been formed consisted of basaltic lavas and (near the sea coast) coral. Both of these materials were essentially basic in character. Hawaiian basalts are composed largely of silica, iron, aluminum, and various bases, principally sodium, calcium, and magnesium (14, 17). Coral is essentially carbonate of lime.

The mechanical and chemical changes due to rainfall, running water, variations in temperature, etc. constitute a process described as weathering. Weathering has resulted in the disintegration and transformation of the rock into soil. The effect of rain water containing various gases has been to partially dissolve the disintegrated fragments thus released so that at an early period of formation the soil must have been quite alkaline (10).

In regions of low rainfall weathering has been slow and the soil remains in an early stage of development. It may still be alkaline. Thus, soils in the Kau region are still alkaline or neutral (10).

In regions of heavier rainfall the bases were carried below the surface soil because of the downward movement of water (6). They also dissolved a large part of the original silica which was also leached out. The result has been a gradual depletion of the soil with respect to silica and the bases sodium, potassium, calcium, and magnesium with a relative enrichment with regard to iron, aluminum, and replaceable hydrogen. As the bases have been removed the soil has become less alkaline.

Gases dissolved in the rain water, acids formed by microorganisms and by decaying vegetation have gradually made the soils more acidic, thus accelerating the removal of bases. This process has gone on at all times and in all places, but most rapidly in regions of warmth, heavy rainfall, and dense vegetation. At the present time a great part of our middle-belt and upland soils are distinctly acid.

Along the sea coast this process has been retarded by the factors of less rainfall and vegetation, but principally by the presence of coral rock fragments. Carbonate of lime (calcium carbonate) is basic, but not very soluble at a pH above 7.0. It is not readily removed by leaching but can still neutralize acids which are formed in the soil over a long period of time (21). Furthermore, coral provides a source for

replaceable calcium. Coral soils thus tend to be alkaline and rich in replaceable calcium.

In the arid regions of the southwestern part of the United States the process of weathering, while slower than in more humid sections, has over many years formed soils which physically may be in a late stage of development. Lack of adequate rainfall has, however, reduced leaching of bases so that at present these soils are saturated with carbonates and sulfates of sodium, calcium, magnesium, etc. These soils are typical alkali soils (7, 10, 20) and are not generally found in Hawaii. We do find, nevertheless, a few soil areas near our sea coasts formed from recently drained salt marshes, etc., which are saturated with saline matter, principally sodium salts. Such soils are alkaline, heavy and sticky. When dry they are hard and tend to crack. Although generally well supplied with plant nutrients, they are not usually very fertile until reclaimed by special treatment.

Effects of Cultivation

Drainage, plowing, and irrigation accelerate the process of soil disintegration and in that way tend to increase soil acidity. At the same time cultivation improves the soil in other respects. Furthermore, the changes take place slowly. The historic period of cultivation has been short compared with the period during which rocks have disintegrated into soils.

Fertilizers and soil amendments have various effects upon soil acidity (19). Sulfate of ammonia and ammophos form acids in the soil due to a process of bacterial attack upon these ammonium compounds. Nitrates of soda and lime, raw rock and probably superphosphate oppose this process since they introduce permanent bases. Lime, ground coral and coral sand directly neutralize soil acidity (21). Saline irrigation water frequently provides ample supplies of replaceable bases, including potassium as shown by one of us (11).

Soil Acidity and Cane Growth

It is a generally recognized fact that plants will not grow well in either very acid or alkaline soils. It is probably safe to say that the amount of total acidity has little direct effect upon growth. On the other hand, soil reaction may be very important, indirectly as well as directly.

The direct effect of low pH has been studied by Martin (13) who grew cane in water cultures which contained fertilizers and were adjusted to various pH values. He discovered increasing evidence of poorer growth below a pH of 5.0, but particularly below 4.0. At pH values higher than 5.0, iron and phosphates were less available and poor growth resulted.

In the soil these conditions may be aggravated by increased solubility of aluminum in acid soils (4). Aluminum has been shown to be toxic in moderately high concentrations. On the other hand, sugar cane may be relatively tolerant to the effects of high acidity when other growth factors are favorable, while poor aeration, lack of sufficient sunlight, water and plant food, infection with *Pythium,* etc. may augment the effect of acidity (9).

A rather important matter remains to be considered. The bases calcium, magnesium, and potassium are essential to plant growth. A soil with high total acidity is a soil partially depleted of these bases. But of more importance is the fact that a soil of this type does not retain these bases adequately when they are applied as fertilizer because hydrogen is not easily replaced by bases except when they are in an alkaline solution. Acid soils have poor fixing power for potassium, etc., and applied fertilizer bases are readily lost by leaching under conditions of heavy rainfall (12). The problems presented by alkaline soils are of a different character. They are usually well supplied with bases and retain applied potash. Iron and manganese are generally less available and chloroses of one type or other may be caused by deficiencies of these elements in available form.

Corrective and Preventative Measures

Excessive alkalinity can be ameliorated by the use of acid-forming fertilizers such as sulfate of ammonia. Commercial yellow sulfur (flowers of sulfur) in the presence of sufficient organic matter will tend to reduce alkalinity (22). Areas of land formed from swamps near the sea can be reclaimed by adequate drainage, including ditches and subsurface drains, and by irrigation. The appropriate type of irrigation water is moderately saline. Sodium-saturated soils are of a heavy type and are only kept open by the presence of some salt in the water. Pure mountain water will render these soils impervious.

It is a matter of common knowledge that excessive acidity can be corrected by applications of lime in one or more of its various forms (21). Lime both neutralizes the acidity and supplies the soil with replaceable calcium. The effect of such treatment is usually beneficial and it is customary in many countries (formerly including Hawaii) to apply large amounts of lime to acid soils.

However, it has been shown by Verret (24) that heavy liming of sugar cane lands probably results in poor juices for the succeeding crop. As a result, liming as an amendment when used in very large quantities on some Hawaiian soils has not been immediately successful and is not practiced so extensively at present as in the past. It is, of course, conceivable that a beneficial effect can be obtained by rather moderate periodic applications of lime. It is probably neither necessary nor desirable to apply sufficient lime to bring the soil to neutrality. A policy which would prevent increase of acidity and maintain a reasonable supply of replaceable (available) calcium appears to be desirable (12). From this point of view, periodic rapid chemical estimations of "available" calcium may be very useful, while determinations of lime requirement would be of little or no advantage.

A tendency for soil acidity to increase can be checked to some extent by the use of fertilizers which are not acid-forming, such as raw rock, bone meal, nitrate of lime, or superphosphate (19). Under certain conditions, organic matter yields bases to the soil upon decomposition. In nature the continuous decomposition of root residues probably has this effect to some extent. However, the influence of organic matter upon soils is very complex, since it depends upon climate, rainfall, the types of microorganisms in the soil, the nature of the organic material and other factors.

An acid soil, low in replaceable bases, in a region of high rainfall does not adequately retain applied potash and ammonia nitrogen. The problem is that of obtaining maximum value from fertilizer by providing it to the crop rather than to the drainage. It has been shown by Ayres (1) and others that at certain periods in the life of the cane there is a maximum tendency to assimilate potash and nitrogen. It is possible that these factors definitely affect the optimum utilization of fertilizers and that questions of time and number of applications are most advantageously considered with due regard to these facts.

At the present time a comprehensive study of soil changes affected by various types of fertilization, particularly with reference to soil acidity, is being pursued by P. L. Gow. It is hoped that an augmented knowledge of the rate of increase or decrease of soil acidity will enable us to predict the outcome of different fertilizer practices over a period of years and to suggest alternative means for controlling undesirable changes.

Summary

1. A general discussion of acidity and alkalinity is presented: Strong acids have certain easily recognized characteristics, such as sour taste. Bases are substances which neutralize acids and acids are substances which neutralize bases.

2. The total acidity of a soil is equivalent (a) to the amount of base required to neutralize the soil, and (b) to the conventional value for replaceable hydrogen.

3. Soil reaction is a characteristic due to the amount of acidity or alkalinity in a specially active form. It is evaluated on the pH scale, with strongly acidic reactions assigned low numbers and alkaline reactions higher numbers.

4. A buffer is a substance in a relatively stable state so that large changes in pH are not readily produced by small or moderate changes in total acidity. Soils are usually highly buffered.

5. Hawaiian soils appear to have been originally alkaline. During the process of weathering and transformation they have tended to become acid with a consequent loss of bases and silica and a relative enrichment with respect to aluminum, iron and replaceable hydrogen. Along the sea coast coral rock has checked this process. Reclaimed salt marsh land is alkaline.

6. Certain fertilizers and soil amendments tend to increase soil acidity; others tend to check it.

7. Excessive acidity or alkalinity may be directly and indirectly deleterious to the growth of sugar cane.

8. Excessive alkalinity may be checked by the use of acid-forming fertilizers or soil amendments. Acidity may be controlled by the use of proper fertilizers and reduced by the use of lime.

9. An acid soil is generally deficient in replaceable bases essential to cane growth and furthermore does not adequately retain applied fertilizer bases. This fact may have an important bearing upon the optimum time and number of applications of such fertilizers.

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The Fluctuations of Sugars in the Leaf Sheaths of the Sugar Cane Plant During the Day and the Night

By Constance E. Hartt

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I. HISTORICAL INTRODUCTION

The Transport of Sugar in Plants is of Fundamental Importance

Questions concerning the origin of cane sugar in the leaf blades of the sugar cane plant were considered in a previous paper (15) on the fluctuations of sugars in the leaf blades of the sugar cane plant during the day and the night. Of equal importance are the many questions to be raised regarding the origin of cane sugar in the millable cane. In what form does the sugar migrate from the blade to the stem? When does the movement or translocation take place? Through which cells does the sugar pass? By what means does the sugar move? What external and internal factors hasten the translocation of sugar, and in that way promote the storage of sugar in the millable cane? Do any of the constituents of fertilizers or soil amendments have an effect upon the rate or efficiency of translocation? What is the effect of irrigation or drying upon the movement of carbohydrates* from the blade to the stem?

Because all sugars in moving from the blade, or place of manufacture, to the stalk or place of storage, must pass through the sheath in some form or other, a study of the variations in the carbohydrates in the sheath during the day and the night was undertaken in an attempt to elucidate some of the problems proposed in the preceding paragraph. The results of our study are offered now as a report of progress and are not intended as an exhaustive study upon which applications should be based. Further studies of a similar nature will be recorded as they mature.

For the non-botanical reader a few explanations regarding the process of translocation are presented as an introduction to the report of the original research.

Translocation is the Movement of Materials Through Plants

The scientific term applied to the migration or movement of dissolved substances through the plant is translocation. This process is as important for the well being of a plant as is the circulation of the blood for the human body. The complex body of a plant such as sugar cane is composed of several kinds of organs each with special functions. For the proper carrying out of these functions every living cell must be supplied with water, essential salts, sugar, and other things. The tiny root tips poking their way deep into the soil must receive a constant supply of sugar to enable them to continue growth. Even the processes of absorption of nitrogen, phosphorus, potassium, etc., by the roots are thought to require a plentiful supply of sugar, inasmuch as they are aided by the energy released in respiration (16). Surplus sugar over and above that used in growth is stored in the stem. As an eye sprouts and forms a young shoot on a cutting, translocation of sugar from the cutting to the growing points of both stem and root is essential. Thus the process of translocation of sugar is of fundamental importance.

Translocation of Sugar Occurs in the Phloem

The question of which cells are responsible for the downward movement of sugar from the leaves to the stems has been studied recently by Mason and Maskell (24),

*For brief definitions of the carbohydrates mentioned in this report, consult the previous paper (15).

who investigated the cotton plant. This is a particularly favorable kind of plant for such studies because of its internal structure. The two tissues which, because of the elongation of their cells, might theoretically form the pathway for translocation (phloem and xylem) are separated in the cotton plant by a thin-walled tissue which breaks easily (the cambium) ; thus a separation of the phloem and xylem can readily be made before analysis. This has been done by Mason and Maskell, who found that sugars fluctuate in the phloem during the day and the night in the same way that they do in the leaves, but that they remain relatively constant in concentration in the xylem. They conclude that the translocation of sugars takes place in the phloem. Curtis (6) also is of this opinion.

The structure of the sugar cane plant differs from that of cotton. In sugar cane, the phloem and xylem occur close together with no separating tissue, and little bundles or groups of phloem and xylem cells are found in the veins and midrib of the blade, in the fibers of the sheath, and scattered throughout the stem. Because of the impossibility of separating the phloem and xylem in sugar cane for the purpose of quantitative analysis, and because the methods for microchemical study are not entirely satisfactory, the determination of the pathway of translocation can not be made well with sugar cane. However, inasmuch as the studies of Curtis and of Mason and Maskell and of others furnish strong evidence that the phloem is the pathway of translocation in other kinds of plants, this seems a safe assumption in sugar cane.

Translocation Occurs Both Day and Night

We are accustomed to think that sugar is made and stored in the blade during the hours of daylight and translocated to the stem during the night. The question arises as to whether some translocation of sugar occurs also during the day. This problem has been studied by Tschesnokov and Bazyrina (33), who found that some kinds of plants carry on translocation chiefly during the night (e. g., the potato), others (e. g., peas) principally during the day. Colin (2) in a study with the sugar beet, found that sugar migrates from the blade to the root by day as well as by night. The question of time of translocation in sugar cane is considered in this report.

What External and Internal Factors Affect the Speed of Translocation of Sugar?

Because of the uncertainty regarding the kind of sugar which is translocated and for other reasons, the factors affecting translocation are not thoroughly understood. Some of the more important factors are the relative amounts of translocatory material, the necessity for living cells in the phloem, length of day, and water content. Many studies with several kinds of plants have shown that in passing from the leaves to the stems, sugars go from a place of low concentration to a place of high concentration, thus against the concentration gradient, or "upstream." A recent illustration of this phenomenon is afforded by the results of Leonard (21), who found that in the sugar beet, cane sugar usually increased continuously from the blades to the roots. The data presented in this paper seem to indicate the same fact, and it is well known that there is more cane sugar in the stem than in the leaf of sugar cane. If cane sugar is a translocatory substance, how can it move against the gradient? Some help in understanding this problem may be obtained from the work of Mason and Maskell (24), who found that the separate analysis of tissues enabled the detection of concentration gradients in the cotton plant, with the sugar

moving with the gradient, or "downstream" in the phloem of the stem. They found that even when sugar moves against the gradient an increased concentration of sugar in the leaf caused an increased rate of translocation to the stem. The same investigators (26) suggest that where the food materials appear to move "upstream," perhaps the "downstream" movement of mobile material is masked by a large amount of storage or immobile material. However, there is at least one place in the cotton plant in which sucrose definitely accumulates against a gradient, and that is in passing from the cells of the mesophyll (or middle, green tissue of the leaf) into the phloem of the fine veins in the leaf, according to Phillis and Mason (29), who have suggested that the transition cells of the fine veins and the companion cells of the phloem are responsible for the accumulation of sucrose against a gradient and probably also for the movement of glucose and fructose against a gradient. They state that their experiments demonstrate that although concentration gradients may determine the direction of movement along the larger veins, yet there are other factors that determine the direction of movement between the mesophyll and the fine veins.

It was recognized very early that living cells are essential for translocation and a review of the evidence indicating that assumption is given by Curtis (6). Thus any condition which coagulates the protoplasm or kills the cells of the phloem will interfere with translocation. It has been shown experimentally that local chilling of the petioles (or leaf stalks) to 0-6° C. interferes with translocation; inasmuch as that temperature is never reached in sugar cane countries the effect of low temperatures in decreasing translocation in the sugar cane plant may be considered insignificant. The application of chloroform has also been found to decrease translocation. Of more importance to sugar cane agriculture is the fact that certain nutritional deficiencies, including boron (17, 18) and potassium (9, 10) have been found to interfere with translocation due to the killing of the protoplasm. Sugar cane undergoing certain nutritional disturbances or growing on acid upland soils may have nodal accumulations of iron and aluminum which occur primarily in the xylem, but which may also have a deleterious effect upon translocation in the phloem, although this point is not definitely established.

Insects have been found to interfere with translocation when they injured the phloem; a specific example is the injury due to leaf miners studied by Schneider-Orelli (31). In sugar cane the insect, *Aphis maidis,* which transmits the virus causing mosaic, punctures the cells of the phloem and obtains food in that way. Thus the amount of food to reach the stem may be decreased. There seems to be no evidence that either the virus or the insect causes an actual plugging of the phloem cells. Such a plugging of the phloem accompanied by discoloration occurs in Sereh, a serious disease of sugar cane absent from Hawaii, which in Java was said to interfere considerably with translocation and to cause depressed growth of certain varieties. Leaf scald disease, which occurs in Hawaii, primarily causes a plugging of the xylem and also occasionally affects the phloem; the causal agent of this disease is *Bacterium albilineans.* Whether or not any insects other than the aphis seek primarily the phloem of sugar cane has not been determined.

The effect of water upon translocation as well as photosynthesis in sugar cane is being studied by the writer and a preliminary report has already been published (12). The sheaths of sugar cane plants deprived of water contained more cane sugar than simple sugar, whereas the sheaths of plants adequately supplied with water con-

tained more simple sugar than cane sugar. It may be that the relative amounts of the sugars in the sheath are affected by the amount of water and thus the translocation form of sugar may be dependent largely upon the moisture content.

Another factor affecting translocation is aeration. Puriewitsch (30) and Grünfeld (8) found that the movement of food to and from the cotyledons or seed leaves is dependent upon aeration. Mason and Phillis (27) state that oxygen starvation seems to affect carbohydrate and nitrogen transport to the same extent.

The Mechanism of Translocation is Unknown

The chief explanations of the mechanism of the translocation of foods which have been suggested by plant physiologists include diffusion, protoplasmic streaming, mass movement, adsorption, and surface tension.

It has been recognized for some time that diffusion alone is an insufficient explanation because the process is too slow to account for the movement of the amount of sugar known to be transferred. In their studies with the cotton plant, Mason and Maskell (25) found that the rate of diffusion of sugar in the sieve tube is about 40,000 times as great as that for sugar in a 2 per cent solution of sucrose in water and is almost identical with the rate of diffusion of molecules the size of sucrose in air. Although diffusion is not the only mechanism, some method similar to diffusion in that it is affected by concentration, is probable, according to Mason and Maskell (24). These authors suggest that there may be a mechanism in the sieve tube which overcomes resistance to diffusion. In a later contribution, Mason and Phillis (27) state that some theory of activated diffusion is needed. They say that the curtailment of oxygen from a limited region of the bark may completely stop the transport of food, which is resumed when the supply of oxygen is renewed. Therefore they suggest that the energy liberated by respiration may activate diffusion by reducing the resistance of the solvent so that diffusion proceeds in the sieve tube at rates comparable with those in a gas.

That the translocation of foods is due to a mass flow caused by differences in pressure has been proposed by Münch (28) and Crafts (3, 4, 5), both of whose systems have been criticised by Curtis (6) and by Mason and Phillis (27). Crafts has suggested that the mass flow of food takes place through the walls of the sieve tubes as well as through the interiors of the cells.

The contents of some cells when viewed through the microscope are seen to be in rapid motion. The protoplasm and chloroplasts (small bodies containing the green pigment chlorophyll) circulate around the cell. This movement is not observed in all cells, possibly because of damage during the preparation of the materials for observation or on account of age or diseased condition of the cell. This motion, called protoplasmic streaming, is sometimes observed in the phloem. If such a movement were universal in active phloem it might carry soluble food from one end of a cell to another far more quickly than can be done by diffusion. The food could then pass through the pores in the end walls (unless these pores are plugged) and be swept rapidly by the streaming protoplasm to the opposite end of the cell. However, the theory that the means of translocation is protoplasmic streaming is not entirely satisfactory, since it does not account for the cause of protoplasmic streaming. Van den Honert (34) has even suggested that the streaming of protoplasm may be the result of translocation rather than its cause. Kok (19) studied the rate of

translocation and concluded that there is no evidence that protoplasmic streaming aids translocation.

One of the simplest theories of translocation is the one recenty proposed by Van den Honert (34), depending upon the fact that things which reduce surface tension between two substances move to the boundary. The speed of such a movement is about of the same order of magnitude as the speed of translocation. This theory is satisfactory not only from the standpoint of speed but also because it is in harmony with the dependence of translocation upon differences in concentration.

Went (36) has suggested that the "growth promoting substance" which is a newly discovered plant hormone essential for growth, may be translocated through the companion cells of the phloem by catephoresis. Catephoresis is the movement of an electrolyte (salt, for example) through a solution through which an electric current is passed, in the direction of one of the poles. Catephoresis results in the accumulation of the electrolyte in one place, and there is a movement from a solution of weak concentration to a highly concentrated location. Electric currents have been found in plants by various investigators and the suggestion has been made that electrical phenomena may aid in the process of translocation. Phillis and Mason (29) remarked that since a non-electrolyte like sugar can be accumulated against a gradient by the fine veins perhaps electrical forces are not at work. The possible effect of electric currents upon translocation has recently been mentioned by Lund (23), who has demonstrated electric circuits between different microscopic points on the same cell. Differences in electric current between larger areas in the stems of sugar cane may be measured by the electrynx, by which the Brix may be estimated, giving a measure of the ripeness of cane. The electrynx is now in use on a few plantations in Hawaii.

According to Crafts (5) a combination of diffusion, protoplasmic streaming, and pressure flow seems to explain translocation in the potato most satisfactorily.

Whether these theories of the mechanism of translocation will be permanently accepted in the literature remains to be seen.

What Kinds of Sugars Are Translocated?

It is known that foods to be translocated must be in solution. Since starch is a solid, it cannot be moved without first being digested to sugar. The question arises as to what is the sugar of transport. Are the simple sugars translocated, or sucrose, or both?

Studies of the translocation forms of sugars have been conducted by many workers with different kinds of plants. Some investigators have presented evidence that the simple sugars are transported, others that cane sugar is transported, and some have favored the view that both the simple sugars and cane sugar may be transported. Lists of the authors favoring each view need not be included here. This subject has been discussed recently by Leonard (20).

With sugar cane, Viswanath (35) in 1919, favored the view that the simple sugars are translocated, whereas Geerligs (7) in 1924 concluded that both cane sugar and the simple sugars are translocated in the sugar cane plant.

II. ORIGINAL RESEARCH

Methods

Details regarding the plants used in this investigation, the methods of sampling and of analysis, have already been recorded (15). The leaf of the sugar cane plant

consists of two distinct portions, the blade and the sheath. The blade is the flat, dark green part which is extended in the air and in which the greater part of the manufacture of food occurs. The sheath is the part which is clasped tightly around the stem. The transport of water and fertilizer elements from the stem to the blade, and the movement of sugars and several other foods from the blade to the stem, are two important functions of the sheath. The sheaths of the same leaves discussed in the former paper were used in this investigation, which really constitutes a continuation of the study of photosynthesis. No analyses of sheaths were made in the June experiment. In the December experiment analyses were made of the midribs removed from the leaves taken at 7 a. m. and at 7 p. m.

Results

The results of the analyses of simple sugars, cane sugar, polysaccharides, and moisture of the sheaths taken in April 1933, are recorded in Table I and Fig. 1. The curves have been smoothed by the method of moving averages, and it is felt that comparisons made with graphs smoothed in this way are more reliable than the original data because this method tends to overcome the effects of individual differences and sampling errors. The results of the analyses of the sheaths taken in the December 1933 experiment are given in Table II and Figs. 2-4. The results of the analyses of the midribs taken in December are presented in Table III. Sunlight records measured by an Eppley pyrheliometer were published in the other paper (15). The results of the December experiment are expressed upon the residual dry-weight basis. The residual dry weight, which is calculated by subtracting the sum of the total sugars plus polysaccharides from the dry weight, remains relatively constant over short periods of time (24-48 hours), and therefore constitutes a more reliable basis for calculations than either the green-weight or the dry-weight basis.

TABLE I

Analyses of sheaths taken in April 1933. Sugars and polysaccharides expressed on moisture-free basis. Also moisture percentages.

Time of sampling	Simple sugars	Cane sugar	Polysaccharides	Moisture
April 25	Per Cent	Per Cent	Per Cent	Per Cent
1 p.m.	3.78±0.002	7.80±0.248	23.17±0.443	79.78±0.066
3	3.29±0.023	7.83±0.019	20.94±0.057	79.19±0.009
5	3.56±0.095	8.99±0.042	21.67±0.128	78.79±0.076
7	3.33±0.009	9.07±0.119	——	80.34±0.076
9	3.82±0.002	8.37±0.009	21.00±0.195	80.72±0.090
11	3.56	9.82	24.78±0.114	80.57±0.171
April 26				
1 a.m.	3.06±0.057	8.57±0.114	23.60±0.057	80.38±0.142
3	3.23±0.009	7.98±0.019	23.33±0.028	80.07±0.195
5	3.96±0.014	10.35±0.119	21.38±0.333	81.97±0.682
6	3.59±0.023	9.01±0.195	20.97±0.162	80.36±0.104
7	3.55±0.019	8.25±0.295	20.94±0.033	79.88±0.066
9	4.36	8.00	21.01	80.10±0.081
11	4.01±0.023	9.22±0.081	24.56±0.205	80.92±0.071

TABLE II

Analyses of sheaths taken in December 1933. Sugars, starch, and polysaccharides expressed on the residual dry-weight basis. Also moisture percentages.

Time of sampling	Simple sugars	Cane sugar	Starch	Polysaccharides	Moisture
December 27	Per Cent	Per Cent	Per Cent	Per Cent	Per Cent
5 a.m.....	9.235±0.135	4.584±0.286	2.329±0.081	31.12±0.622	85.84±0.023
6	10.505±0.131	2.866±0.216	1.723±0.008	26.22±0.257	85.67±0.009
7	11.577±0.074	7.436±0.210	2.075±0.023	27.99±0.350	86.35±0.028
8	9.255±0.051	6.323±0.471	2.197±0.042	29.78±0.340	85.56
9	9.235±0.216	5.271±0.011	2.298±0.086	28.93±1.207	85.71±0.429
11	9.929±0.106	5.441±0.453	3.587±0.207	42.40±1.358	85.00±0.124
1 p.m.....	10.595±0.020	7.376±0.268	2.670±0.032	40.03±0.033	85.40±0.124
3	9.903±0.150	7.827±0.279	3.414±0.155	36.85±0.125	85.57
5	8.397±0.102	7.044±0.048	3.017±0.050	39.06±0.100	84.09±0.033
6	9.700±0.199	7.993±0.162	2.572±0.045	40.14±1.321	85.58±0.038
7	9.138±0.125	7.614±0.154	2.897±0.003	37.87±0.904	85.01±0.090
9	9.719±0.056	6.935±0.054	2.663±0.024	40.45±0.381	84.93
11	——	——	3.487	38.69±0.319	85.12±0.038
December 28					
1 a.m.....	8.403±0.051	5.851±0.297	2.528±0.079	39.22±0.079	85.37±0.057
3	7.611±0.044	4.353±0.035	2.460±0.105	30.85±0.074	85.18±0.038
5	9.720±0.122	5.421±0.169	2.425±0.015	38.13±0.098	85.33±0.071
6	10.740±0.340	5.257±0.280	2.789±0.006	34.25±0.223	85.54±0.019
7	9.017±0.106	5.424±0.093	2.224±0.027	28.79±0.904	85.39±0.066
8	7.261±0.144	5.282±0.129	2.023±0.040	29.19±1.307	84.77±0.081
9	7.694±0.079	4.372±0.149	1.957±0.023	31.89±0.212	84.99±0.085
11	8.030±0.112	5.128±0.089	2.015±0.023	28.29±0.508	83.81±0.019

TABLE III

Analyses of midribs taken in December 1933. Sugars, starch, and polysaccharides expressed on residual dry-weight basis. Also moisture percentages.

Time of sampling	Simple sugars	Cane sugar	Starch	Polysaccharides	Moisture
December 27	Per Cent	Per Cent	Per Cent	Per Cent	Per Cent
7 a.m.....	2.617±0.006	2.711±0.179	0.568	24.83±0.438	77.76±0.023
7 p.m.....	3.503	6.274	0.468	22.98	77.18±0.081
December 28					
7 a.m.....	3.580±0.042	2.975±0.382	0.594	24.06±0.400	77.68±0.181

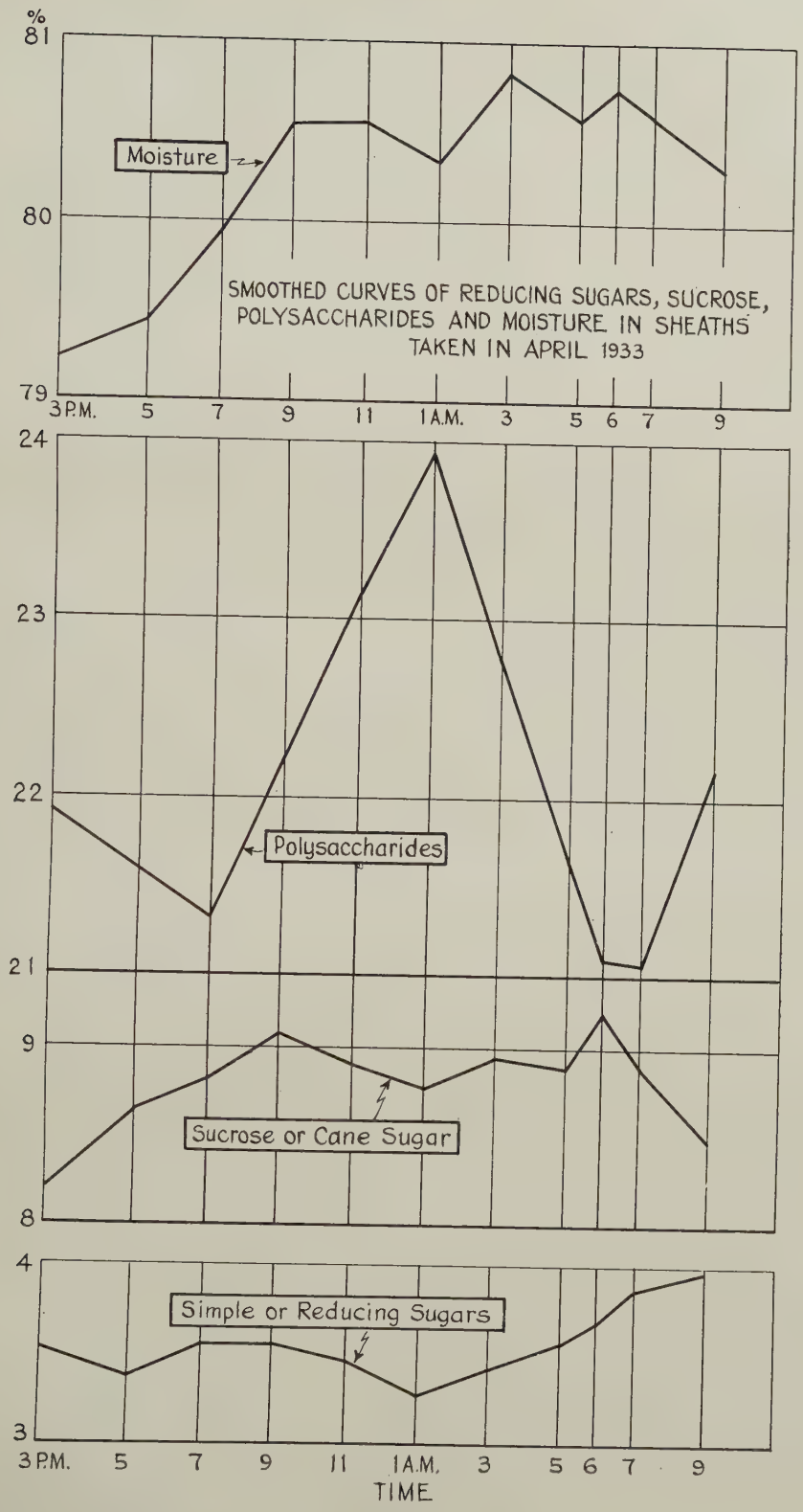
%
81
80
79
Moisture
SMOOTHED CURVES OF REDUCING SUGARS, SUCROSE, POLYSACCHARIDES AND MOISTURE IN SHEATHS TAKEN IN APRIL 1933
3 P.M. 5 7 9 11 1 A.M. 3 5 6 7 9
24
23
22
21
9
8
Polysaccharides
Sucrose or Cane Sugar
4
3
Simple or Reducing Sugars
3 P.M. 5 7 9 11 1 A.M. 3 5 6 7 9
TIME

Fig. 1.

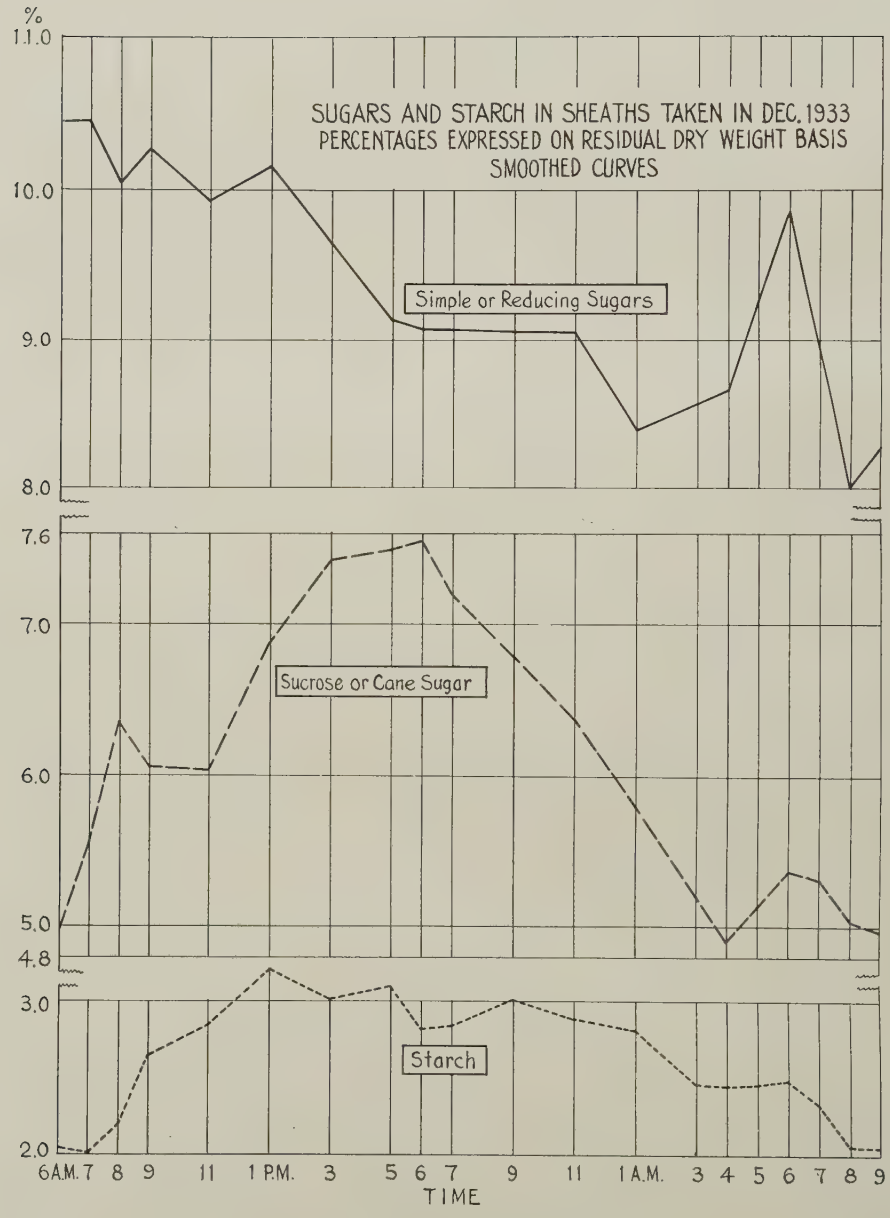
%
11.0
10.0
9.0
8.0
SUGARS AND STARCH IN SHEATHS TAKEN IN DEC. 1933
PERCENTAGES EXPRESSED ON RESIDUAL DRY WEIGHT BASIS
SMOOTHED CURVES
Simple or Reducing Sugars
7.6
7.0
6.0
5.0
4.8
Sucrose or Cane Sugar
3.0
2.0
Starch
6A.M. 7 8 9 11 1 P.M. 3 5 6 7 9 11 1 A.M. 3 4 5 6 7 8 9
TIME

Fig. 2.

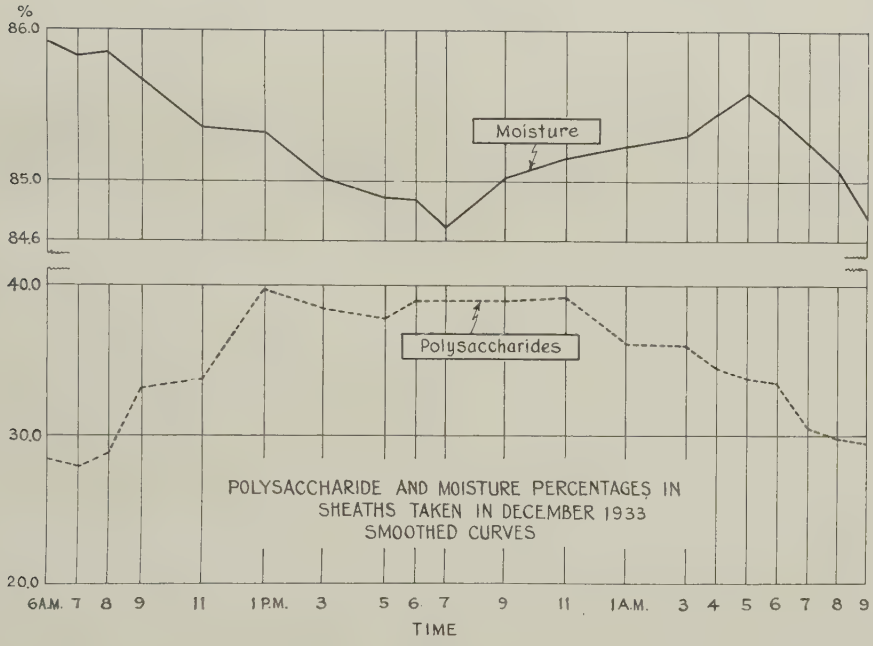
%
86.0
85.0
84.6
Moisture
40.0
30.0
20.0
Polysaccharides
POLYSACCHARIDE AND MOISTURE PERCENTAGES IN
SHEATHS TAKEN IN DECEMBER 1933
SMOOTHED CURVES
6A.M. 7 8 9 11 1P.M. 3 5 6 7 9 11 1A.M. 3 4 5 6 7 8 9
TIME

Fig. 3.

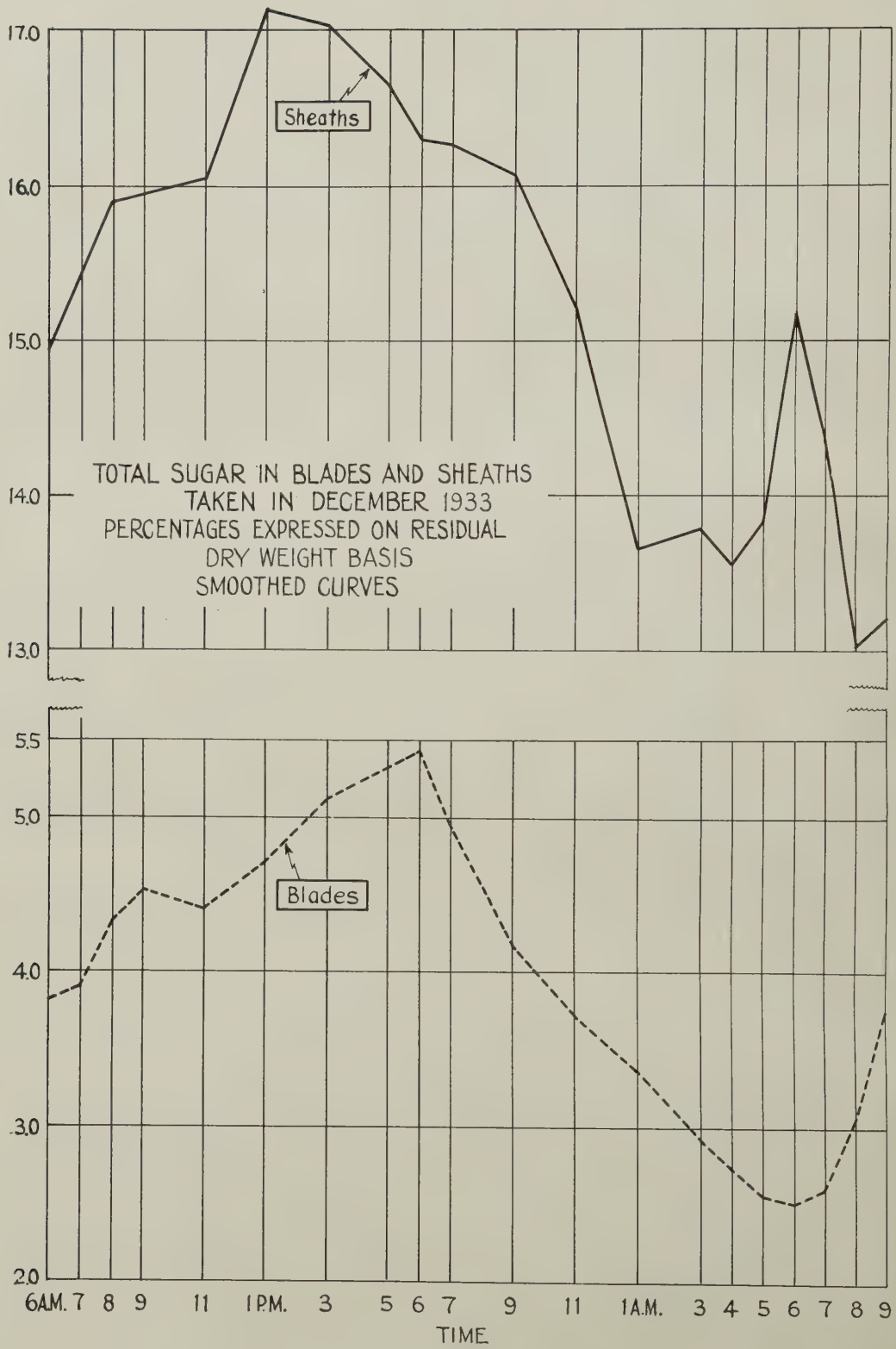
17.0
16.0
15.0
14.0
13.0
Sheaths
TOTAL SUGAR IN BLADES AND SHEATHS
TAKEN IN DECEMBER 1933
PERCENTAGES EXPRESSED ON RESIDUAL
DRY WEIGHT BASIS
SMOOTHED CURVES
5.5
5.0
4.0
3.0
2.0
Blades
6A.M. 7 8 9 11 1P.M. 3 5 6 7 9 11 1A.M. 3 4 5 6 7 8 9
TIME

Fig. 4.

Discussion

Moisture:

The water content of the sheaths of the sugar cane plant fluctuates during the day and the night, as shown in Figs. 1 and 3. In the April experiment the moisture percentage rose until 9 p. m. and then remained nearly constant, showing minor fluctuations during the night, and suggesting a decrease in the morning. In the December experiment the moisture content decreased steadily from 6 a. m. until 7 p. m., and then increased until 5 a. m., followed by a decrease until 9 a. m., which was the end of the experiment. Thus the course of the curves for moisture content of the sheaths differed in the two experiments, and both differed from the curves for moisture in the blades (15). They are alike in that both experiments show higher percentages of moisture in the sheaths than in the blades, which may be a point of importance in translocation.

The percentage of moisture in the sheaths exhibited less variation than that in the blades. In the April experiment, the moisture percentage of the sheaths varied from 79 to 81 per cent in round numbers, whereas in the blades the percentage of water varied from about 67 to 70 per cent. In the December experiment, the moisture percentages of the sheaths varied from about 85 to 86 per cent, whereas in the blades the variation lay between 70 and 74 per cent. It would seem that the moisture content of the sheaths is affected by the time of the day less than is the moisture content of the blades. This is only to be expected, since the sheaths are considerably more protected than the blades.

Why did the percentage of moisture in the sheaths remain nearly constant during the night in the April experiment, whereas in the December experiment an increase occurred until 5 a.m.? The moisture percentages of the blades in both experiments showed low points at 3 p.m., high points at 5 a.m., and breaks in the rise during the night. With these similarities in the blades, why did the sheaths differ? The two experiments differed in the age of the plants and in the season. Differences in season (i.e., in temperature and clouds, which affect the rate of loss of water from leaves) were probably responsible for the greater moisture content of the plants taken in December than those taken in April. The plants used in the December experiment were only six months old, while those in April were 10 months of age. Perhaps the sheaths of the younger plants were not as highly cutinized (covered by a thin wax-like coating) as those of the older plants, and thus were more sensitive; or else there may have been some unknown factor responsible for this difference.

Cane sugar:

The percentage of sucrose or cane sugar in the sheaths taken in April increased until 9 p.m., remained fairly constant until 6 a.m., and then decreased at least until 9 a.m., as shown in Fig. 1. In the December experiment the cane sugar increased, with some fluctuation, until 6 p.m., decreased until 4 a.m., increased slightly until 6 a.m., and then decreased to 9 a.m., according to Fig. 2. Thus in April the curve for cane sugar in the sheaths resembled that for moisture; but in December the curve for cane sugar in the sheaths resembled that for cane sugar in the blades. Undoubtedly it would be of great interest to understand the full significance of these differences, but at present we are unable to do so.

The content of cane sugar in the sheaths taken in April varied from 8 to 9 per cent on the dry-weight basis; that in the sheaths of the December experiment varied from 5 to 7.6 per cent on the residual dry-weight basis (which gives larger figures than the dry-weight basis). Why was there more cane sugar in the sheaths studied in April than in those taken in December? The answer probably involves both age and moisture content, as well as the fact that more sucrose could be supplied by the blades in the April than in the December experiment. Older leaves generally contain more cane sugar than younger leaves. The sheaths taken in December had higher percentages of moisture than those taken in April; inasmuch as the former also had higher percentages of simple sugars than the latter, it would seem that there was greater digestion of cane sugar to simple sugars in the sheaths containing the greater moisture content since the process of digestion is a union with water. This seems a satisfactory explanation of the lower sucrose content in the sheaths in the December experiment than in the April experiment. A necessary corollary is that at least part of the cane sugar in the sheaths studied in December was removed by digestion rather than by translocation.

The question may arise as to whether any of the fluctuations in cane sugar or simple sugars in the sheaths may be due to photosynthesis in the sheaths. It will be remembered that the green pigment chlorophyll is absolutely essential for the manufacture of food by plants. The sheaths used in these experiments were covered throughout the greater part of their length by other sheaths and therefore were for the most part white or yellowish in color. The small amount of chlorophyll in the exposed portions of the sheaths was insignificant, as shown by the fact that the alcoholic solutions prepared from the sheaths were yellow in color, while those prepared from the blades were a rich, deep green with strong fluorescence (reddish glow). Moreover, it has been shown recently (22) that the amount of photosynthesis conducted by the sheaths of grasses is negligible (and sugar cane is of course a grass). Therefore the fluctuations in sugars in the sheaths were due to factors other than photosynthesis in the sheaths.

Simple Sugars:

The curves for simple sugars in the sheaths differed considerably in the two experiments. This should probably be expected, since the content of simple sugars in the sheaths is dependent upon many factors. For this reason the two curves will be considered separately.

In the April experiment the simple sugars showed low points at 5 p.m., and at 1 a.m., according to Fig. 1. After 1 a.m., there was a uniform rise until 9 a.m. In some respects the curve seems related to the curve for polysaccharides. At 1 a.m., the simple sugars were at a minimum while polysaccharides were at a maximum, which may indicate a condensation of simple sugars to polysaccharides. Then after 1 a.m., there was a simultaneous decrease in polysaccharides and increase in simple sugars, which may have been due to the digestion of polysaccharides. Such a conversion of simple sugars to polysaccharides would of course remove them from solution which might be an aid in the translocation of additional sugars from the blades.

In the December experiment a very different picture is presented. The greatest percentage of simple sugars occurred at 7 a.m., as shown in Fig. 2; this was followed

by a decrease with some irregularity until 3 a.m.; an increase to another maximum at 6 a.m., and a decrease to 8 a.m. Evidently some cause led to the nearly constant removal of simple sugars from the sheaths until about 3 a.m., when another stronger factor set in resulting in the accumulation of simple sugars in the sheaths until 6 a.m.

In both experiments there was a greater concentration of simple sugars in the sheaths than in the blades, a subject to be discussed more fully below.

As mentioned under *Cane sugar,* there was more cane sugar than simple sugar in the sheaths taken in April, but in the December experiment there was more simple sugar than cane sugar. This may have been due largely to the greater percentage of moisture in the sheaths taken in December, leading to greater hydrolysis or digestion of sucrose than in the April experiment.

Polysaccharides:

The most striking feature of the curve for polysaccharides in the April experiment is the maximum at 1 a.m., shown in Fig. 1. Because it occurs at the time of minimum concentration of simple sugars in the sheaths and minimum concentration of polysaccharides in the blades, one is led to the conclusion that the polysaccharides are removed from the blades during the night by hydrolysis and subsequent translocation of simple sugars, some of which upon reaching the sheaths are converted into polysaccharides again. Such a temporary storage of polysaccharides in the sheaths during the night might be of considerable importance in removing carbohydrates temporarily from solution thus permitting the continued translocation of soluble carbohydrates from the blades into the sheaths.

In the December experiment, polysaccharides in the sheaths rose to a maximum at 1 p.m., remained high until 11 p.m., and then decreased until 9 a.m., according to Fig. 3. Here again there seems to be a relationship between the period of high concentration of polysaccharides (1-11 p.m.) and a period of decreasing concentration of simple sugars (1 p.m.-3 a.m.), which may indicate a conversion of simple sugars to polysaccharides for temporary storage during the afternoon and night. Some factor caused a rapid increase in simple sugars beginning about 3 a.m. The cause may have been a complex of factors, including the more rapid increase in water content beginning at 3 a.m., and also the decrease in polysaccharides in the sheaths which began after 11 p.m. It is suggested that due to the high but decreasing content of simple sugars in the sheaths in the early morning, a condensation of simple sugars occurred resulting in the formation of polysaccharides. This condensation by removing soluble sugars from solution permitted further translocation from the blades to the sheaths. Simple sugars may also have been continuously leaving the sheaths. Loss of simple sugars by translocation out of the sheaths and by condensation resulted in a minimum concentration of simple sugars. When, however, the amount of simple sugars coming in from the blades plus the amount resulting from the hydrolysis of polysaccharides, surpassed the amount removed from the sheaths by translocation, an increase in their concentration in the sheaths occurred.

A comparison of the curve for polysaccharides in the sheaths with that in the blades (15) shows that the concentration of polysaccharides remained high in the sheaths longer than it did in the blades. This is only natural on the assumption

that a temporary storage of polysaccharides in the sheaths aids in their removal from the blades.

Thus the study of the fluctuations of polysaccharides in the sheaths during the day and the night indicates that the simple sugars are translocated and that a temporary storage of polysaccharides in the sheaths during the night aids in the transportation of carbohydrates from the blades to the stems.

Starch:

Starch was determined in the December experiment only. As shown in Fig. 2, starch increased from 7 a.m. until 1 p.m., and then decreased irregularly until 9 a.m. the following morning. Starch was present in much smaller amounts than the polysaccharides as a whole, indicating the presence in sugar cane of polysaccharides of much greater importance than starch. The curve for starch resembles the curve for polysaccharides as a whole, but is not identical with it.

What is the Translocation Form of Sugar in the Sugar Cane Plant?

The question at issue is as follows: Is sucrose transported from the blade to the stem, or are the simple sugars translocated, or are both cane sugar and the simple sugars translocated in the sugar cane plant? To study these problems it is necessary to consult the previous paper dealing with the blades (15) as well as the data presented in this report.

We now aim to show from a consideration of the data presented in the two reports that both cane sugar and the simple sugars are translocated in the sugar cane plant.

First let us consider the smoothed curves for total sugars in the blades and the sheaths of the December experiment, as shown in Fig. 4. In the sheaths, the total sugars (cane sugar+simple sugars, estimated as invert sugar) increased in amount from 6 a.m. to 1 p.m., decreased to 1 a.m., remained nearly constant in value until 5 a.m., increased to a second maximum at 6 a.m., decreased to a minimum at 8 a.m., and then increased. These trends will now be considered step by step.

What caused the increase in total sugars in the sheaths from 6 a.m. to 1 p.m.? The possible causes of this increase include the following: (1) photosynthesis in the sheaths, (2) formation of sugar in the sheaths from pre-existing carbohydrates already there, (3) translocation of simple sugars out of the blades, and (4) translocation of cane sugar from the blades. These possibilities will now be considered separately. First, regarding the suggestion of photosynthesis in the sheaths, this may take place only to a slight extent because of the small content of chlorophyll. Second, the suggestion of the formation of sugar in the sheaths from pre-existing carbohydrates already present, is not supported by evidence, because starch and other polysaccharides (the carbohydrates from which sugars might be formed) were both also increasing at the same time with the increase in sugar content. The third suggestion, namely, the translocation of simple sugars from the blades (which we think occurred, as mentioned elsewhere) was probably not the immediate cause of the increase in total sugars, because the simple sugars were decreasing in the sheaths at that time. It is possible that simple sugars coming from the blades were transformed in part into cane sugar in the sheaths; it is, however, unlikely that this

is the sole explanation of the increased sugar content of the sheaths, because as shown in Fig. 5 the relative proportions of the simple and cane sugars remained remarkably uniform in the sheaths throughout the day and the night. There thus remains as the most probable cause of the increased sugar content of the sheaths from 6 a.m. to 1 p.m., the translocation of cane sugar from the blades to the sheaths.

It is also probable that a translocation of simple sugars from the blades to the sheaths occurred from 6 a.m. to 1 p.m. for the following reason. Starch and total polysaccharides in the sheaths increased from 7 a.m. to 1 p.m. Since polysaccharides are not translocatable, their increase must have been caused by a condensation of sugars. Although several workers (1, 32) have presented evidence indicating an interconversion of sucrose and starch, yet it is generally recognized that the chief sugars which condense to form polysaccharides are the simple sugars. Now it is possible that some of the sucrose translocated from the blades was inverted to simple sugars, thus furnishing a supply of simple sugars for condensation to polysaccharides. But the curves show an increase in sucrose and a decrease in simple sugars at that time, thus there is no evidence of a marked inversion of sucrose to simple sugars from 6 a.m. to 1 p.m., the time under consideration. It would seem more probable that the increase in starch and other polysaccharides in the sheaths was due to a condensation of the simple sugars supplied by the blades. Polysaccharides increased from 30 to 40 per cent at that time, whereas simple sugars decreased less than 1 per cent. Because the decrease in simple sugars was not enough to account for the increase in polysaccharides, it seems probable that a translocation of simple sugars from the blades to the sheaths occurred from 6 a.m. to 1 p.m.

Thus it is suggested that both cane sugar and the simple sugars are translocated from the blades to the sheaths during the morning. This is a reasonable expectation, inasmuch as photosynthesis is rapid at that time, insuring a plentiful supply of sugars in the blades, whichever sugar is made first. The increase in simple sugars and sucrose which occurs in the blades during the morning is considered to be the surplus over that which is translocated at the same time.

What caused the decrease in the total sugar content of the sheaths from 1 p.m. to 6 p.m.? It is obvious that this decrease in total sugars is due to the fact that the simple sugars decreased in amount more than cane sugar increased at that time. An examination of some of the life processes of the plant may help in obtaining a physiological explanation of this decrease in total sugars. Two main possibilities occur: (1) perhaps translocation of sugar from the blades ceased after 1 p.m., or (2) utilization and export of sugar from the sheaths may have exceeded the import. The first possibility seems unlikely to the author because cane sugar continued to increase in the blades until 6 p.m., which would seem to indicate a plentiful supply for translocation. Also, sucrose increased in the sheaths until 6 p.m., even though the total sugars decreased after 1 p.m. Thus as long as sucrose accumulated in the blades it also increased in the sheaths. Therefore it would seem reasonable to assume a translocation of sucrose from the blades to the sheaths until 6 p.m., rendering it unlikely that the decrease in total sugars at that time was caused by a cessation in the translocation of sugars from the blades.

The other possible cause of the decrease in the total sugar content of the sheaths from 1 to 6 p.m., namely, that the utilization and export of sugar from the sheaths exceeded the import of sugar into the sheaths, may have been due to three causes:

(*a*) the formation of starch and other polysaccharides from the sugars, (*b*) the utilization of the sugar in the sheaths for growth and respiration, or (*c*) greater translocation into the stems. The cause could not lie in the formation of starch and other polysaccharides from the sugar in the sheaths, because starch decreased at that time and total polysaccharides remained the same or perhaps decreased. Neither is it likely to be due to greater utilization of sugar in growth, because it is generally considered that growth takes place chiefly at night, and because there is no reason for assuming so much greater rate of growth after 1 p.m. than before. While one might assume a greater rate of respiration from 11 a.m. to 3 p.m., because of the increased temperature and the fact that heat increases respiration, yet this does not seem a probable assumption for the period 1 p.m. to 6 p.m., because of the falling temperature. Therefore it does not seem likely that all of the decrease in sugar in the sheaths from 1 to 6 p.m. was due to utilization in the sheaths.

The third possibility, that of greater translocation of sugar from the sheaths to the stems, being the only remaining possibility, would seem to be the chief explanation of the greater export than import of sugar in the sheaths from 1 to 6 p.m. This, however, is of no help to us in our main problem (to find which sugar is translocated) inasmuch as it is equally possible that the simple sugars were translocated as such, or that they were converted into sucrose before translocation. However, since there is evidence that both cane sugar and the simple sugars were translocated from the blades to the sheaths during the morning, it seems possible that they were also both translocated from the sheaths to the stems during the afternoon, although it is impossible to prove it from the data at hand.

What caused the decrease in total sugars in the sheaths from 6 p.m. to 1 a.m.? It is not likely that sugar had ceased entering from the blades, although the amount coming from the blades may have decreased because photosynthesis had stopped. That sugar was passing from the blades to the sheaths after 6 p.m. is strongly indicated by the break in the decrease in sugar in the sheaths which occurred at 6 p.m. coincident with the start of the decrease in the sugar content of the blades. Therefore we may assume that the export of sugar from the sheaths was greater than the import, from 6 p.m. to 1 a.m. Determination of the cause of the greater outgo during this period is not as simple as during the previous period. We know that considerable sugar must be used in growth at this time, because of the general assumption that growth takes place chiefly at night, and because the growing region of a cane leaf is the lower part of the sheath. However, it is unlikely that utilization in place can account for all of the decrease in the sheaths, because we know that considerable sugar eventually reaches the stem, although no analyses of stems were performed in this study. Some slight formation of starch may have occurred, as starch showed a slight but unimportant increase from 6 to 9 p.m. However, the general trend was a decrease in starch, and polysaccharides remained the same from 6 to 11 p.m. and then decreased; therefore it is improbable that the decrease in total sugars was due chiefly to condensation. In short, the suggestion is made that between 6 p.m. and 1 a.m. sugar was used in respiration, growth, and in translocation.

Having shown that a translocation of sugar from sheaths to stems may have occurred from 6 p.m. to 1 a.m., there follows the question as to which sugar was translocated. Now it is interesting that from 6 to 7 p.m. coincident with the first marked decrease in cane sugar in the blades, an increase in simple sugars was found.

This indicates hydrolysis of sucrose in the blades. At that time the simple sugar content of the sheaths discontinued its decrease and remained nearly constant, which is only to be expected if the sheaths were receiving a steady supply of simple sugars from the blades. Thus it would seem that in this experiment sucrose was translocated into the sheaths as long as there was a supply available in the blades, and that during the night the simple sugars were translocated more than sucrose.

From 1 to 5 a.m. the total sugar content of the sheaths remained about the same in amount. This is because the increase in simple sugars was nearly equivalent to the decrease in cane sugar. However, it does not necessarily follow that translocation had ceased, even though the total sugar content remained almost constant. It is possible that both types of sugars were passing on to the stems, and at the same time another process was furnishing a further supply of simple sugars. An idea of this other process may be obtained by an examination of the curves for starch and total polysaccharides, given in Figs. 2 and 3. The sharp decrease in starch from 1 to 3 a.m. probably caused the increase in simple sugars at that time, inasmuch as the hydrolysis of starch leads to the formation of glucose. Considerable hydrolysis of polysaccharides took place after 3 a.m., which would also result in an increase in simple sugars. It seems probable that this hydrolysis of polysaccharides caused the large increase in simple sugars which reached a maximum at 6 a.m., as well as the smaller increase in cane sugar which reached a maximum at the same time. In all probability this early morning increase in sugars represents the surplus over that translocated, inasmuch as there is no good reason for supposing a cessation of translocation at 1 a.m. The results of this investigation neither prove nor disprove the translocation of simple sugars between 1 and 6 a.m. or of cane sugar between 4 and 6 a.m.

After 6 a.m., the total sugar content decreased to a minimum at 8 a.m. This decrease may be explained on the assumption that the greater part of the sugars produced by the hydrolysis of polysaccharides had already been removed by translocation. With the source of supply of sugars diminished by lack of photosynthesis and decreased hydrolysis, export was then greater than import, and the result was a sharp decrease in total sugar content, with both sucrose and the simple sugars lessening in amount. The sugar content of the sheaths increased after 8 a.m., probably because photosynthesis had again furnished a supply of sugars which moved down from the blades.

To sum up, it is suggested that both sucrose and the simple sugars are translocated in sugar cane, that translocation takes place both day and night, and that a temporary storage of polysaccharides in the sheaths aids in the translocation of carbohydrates.

The Sucrose Reducing Sugar Ratios in Blades and Sheaths:

The ratios between cane sugar and the simple sugars are plotted in Fig. 5 for the April experiment and in Fig. 6 for the December experiment. The December experiment will be considered first because of its longer duration.

In the blades, the ratio was greater than unity at all but two times (4 and 6 a.m.), whereas in the sheaths the ratio was always less than unity. This illustrates in

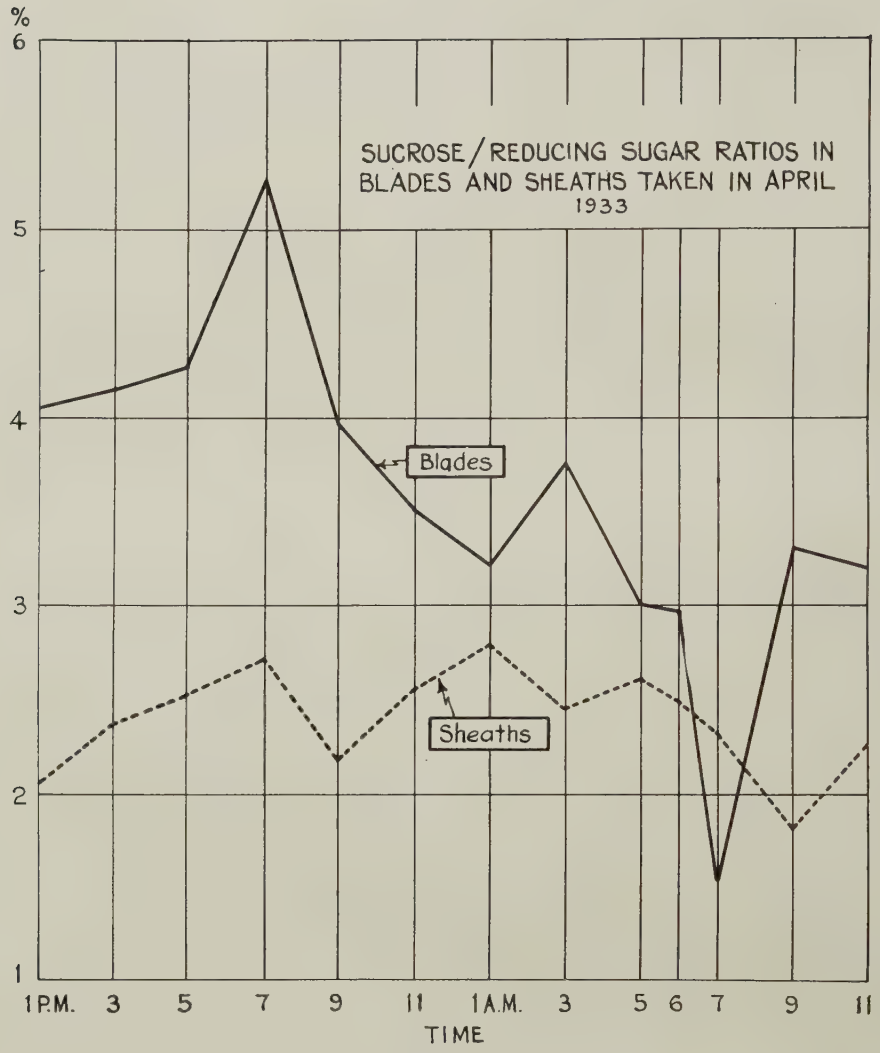

Fig. 5.

striking fashion the predominance of cane sugar over simple sugars in the blades, and the reverse in the sheaths, in the December experiment.

In the blades, the ratio showed no marked tendency up to 3 p.m., fluctuating irregularly but remaining about the same level, indicating no regular change in the relative amounts of the sugars. From 3 to 6 p.m., however, the ratio shows a marked increase, due to the advance in sucrose accompanied by a decline in simple sugars. The curve then falls irregularly from 6 p.m. to 6 a.m., and then rises to 11 a.m. Thus the ratio between cane sugar and the simple sugar in the blades is affected by time of day and probably by light.

In the sheaths, the ratio fluctuates much less than in the blades and is affected little if any by light. The fact that the ratio shows little variation in the sheaths would indicate that there is not much change in the relative amounts of the sugars in the sheaths. In other words, neither formation nor digestion of sucrose is pre-

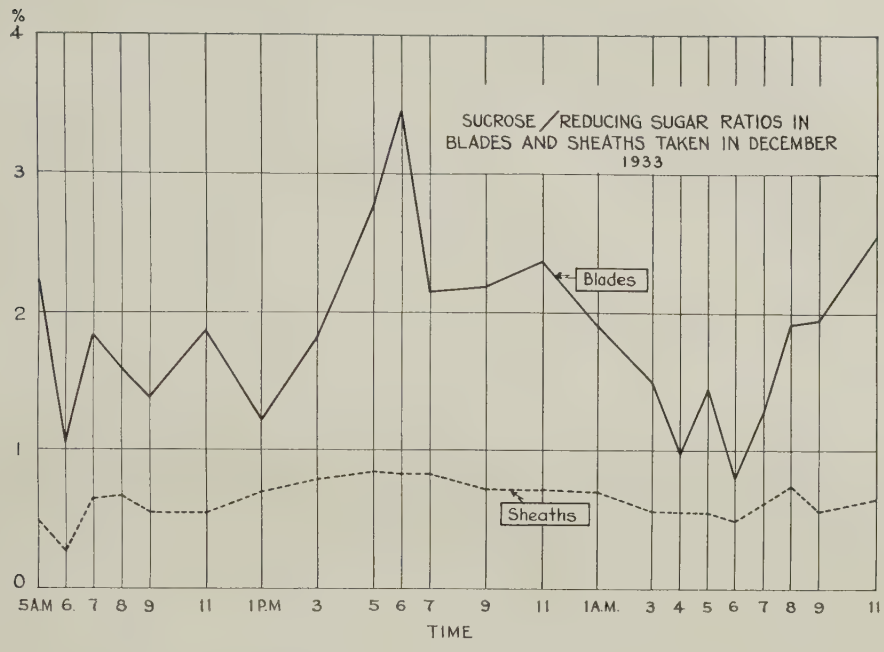

Fig. 6.

dominant in the sheaths; but if some other factor causes a great increase in one kind of sugar, equilibrium is reached again quickly in such a way that there is never any marked fluctuation in the relative amounts of the sugars in the sheaths. This may indicate an important function of the active enzyme invertase often found in the sheaths of sugar cane, to maintain the equilibrium between the sugars.

In the December experiment just discussed there was always more simple sugar than cane sugar in the sheaths, but in the April experiment there was always more sucrose than simple sugars, as shown in Figs. 1 and 5. The April experiment, however, also showed less fluctuation in relation to light in the sheaths than in the blades. Thus whichever kind of sugar is the more abundant, their relative amounts change very little in the sheaths during the day and the night.

Sugar Gradients:

One of the many interesting questions connected with the translocation of sugar is the effect of the concentration of sugar in the blades upon its translocation through the sheaths into the stems. In passing from the blades to the sheaths to the stems, does sugar move with the diffusion gradient ("downstream") or against the gradient ("upstream")?

The data presented in Tables I and II reveal the fact that both cane sugar and the simple sugars in passing from the blades to the sheaths seem to be passing from a place of lower concentration to a place of higher concentration, when considered on the dry-weight or the residual dry-weight basis.

To study this problem further, the results were recalculated and expressed as grams sugar per 100 grams water. When calculated by this method it was found that in the April experiment both cane sugar and the simple sugars were always

higher in the sheaths than in the blades. In the December experiment, the simple sugars were always greater in the sheaths than in the blades; but cane sugar was greater in the blades than in the sheaths at 12 sampling hours, and less in the blades than in the sheaths at eight sampling hours. Thus even when the concentration of sugar in the water is considered, sugar seems to move "upstream" more often than not.

The results of the December experiment recalculated upon the water basis, for the three hours when the midribs were studied, are presented in Table IV, which shows that the simple sugar content of the midribs was intermediate between that of the blades and the sheaths, with the least sugar in the blades, at these three hours. The cane sugar content of the midribs, on the other hand, was at one time the least, at one time the most, and at one time intermediate. This seems to offer no help in the study of sugar gradients.

TABLE IV

The concentration of sugars in blades, midribs, and sheaths, expressed as grams sugar per 100 grams water.

Time	Blades	Midribs	Sheaths
	Simple sugars		
7 a.m.	.394	.576	1.257
7 p.m.	.318	.758	1.041
7 a.m.	.352	.812	1.077
	Cane sugar		
7 a.m.	.734	.603	.656
7 p.m.	1.018	1.532	.891
7 a.m.	.439	.629	.643

The problem of sugar gradients has been mentioned in another report (12), ". . . and the suggestion made that sugars may never actually pass from a cell containing less sugar to one containing more. In both sheaths and stems there is more storage tissue than phloem, and both sheaths and stems have relatively more storage tissue than do blades. The greater percentages of sucrose and reducing sugars in the sheaths and stems than in the blades may be due to the fact that the sugar in the sheaths and stems is spread out in more cells, in which case the direction of translocation would be with the diffusion gradient."

What Factors Affect the Translocation of Sugar in the Sugar Cane Plant?

Only a beginning can be made in the treatment of this problem, which has not yet been studied adequately. Among the factors which affect the process of translocation in sugar cane the following may be mentioned; insects and diseases, potassium deficiency, the condition of the phloem, the activity of invertase and other enzymes, the supply of sugar, the temporary storage of polysaccharides, and the moisture percentage. The first three of these factors were discussed in the introduction.

The importance of enzymes in facilitating the translocation of foods in the sugar cane plant depends upon the fact that many foods must be digested before they can be translocated, and enzymes are essential for the process of digestion. The im-

portance of enzymes in the growth and nutrition of plants has already been discussed elsewhere (14). Insoluble foods such as starch and other polysaccharides cannot move from place to place in the plant without first being changed to soluble forms, and this change requires the aid of specific enzymes. An illustration of the importance of enzymes in translocation may be taken from a hitherto unpublished experiment in which the activity of the enzyme amylase (starch-splitting) in the growing point of Uba cane was found to be weaker than that of six other varieties of sugar cane, growing side by side. It is suggested that the weaker activity of amylase in the growing point of Uba cane may aid in explaining the failure of starch to disappear from the stalk of that variety of sugar cane. With more active amylase the insoluble starch could be digested to a soluble sugar and be used in translocation, storage, or growth.

The importance of invertase in aiding the translocation of sugar has already been mentioned. Because the ratio between cane sugar and the simple sugars in the sheaths remains nearly constant during the day and the night, it is suggested that when some factor causes a decided increase or decrease in one kind of sugar, equilibrium is reached again quickly due to the active invertase which has been found to be of general occurrence in the sheaths of the sugar cane plant.

The necessity for a supply of sugar for translocation may be taken as axiomatic. The more sugar there is made in the leaf the more there is available for translocation, unless some other factor becomes limiting. Thus it is only natural that during a cold, rainy, cloudy season less sugar is translocated to the stems than during a warm sunny period, because under the former conditions the formation of sugar is diminished on account of the decreased rate of photosynthesis. Of course other processes besides photosynthesis and translocation are affected by such factors as temperature, rain, etc., and in the final analysis, the amount of sugar available for translocation from the blades is the surplus over that used within the blades.

What has just been said for sugar in general would seem to apply to the translocation of specific sugars. It has been suggested above that in the December experiment cane sugar was translocated into the sheaths as long as there was a supply available in the blades, and that during the night the simple sugars were translocated more than sucrose merely because the hydrolysis of polysaccharides in the blades during the night furnished a greater supply of simple sugars than of cane sugar for translocation.

Thus there are two main sources of supply of sugar for translocation: photosynthesis, which is limited to the daylight hours; and the digestion of polysaccharides, which occurs chiefly during the night.

The formation of polysaccharides in the blades occurs during the day as a secondary result of photosynthesis. The manufacture of the insoluble starch and other insoluble polysaccharides removes considerable quantities of soluble sugars from solution. This is important inasmuch as the accumulation of all the soluble sugars formed in photosynthesis might interfere with that process seriously since the accumulation of the end products of a chemical reaction is known to decrease the speed of that reaction. The temporary storage of polysaccharides in the blades during the day aids in translocation by furnishing a supply of sugars for translocation after nightfall, when photosynthesis stops. This suggestion is based upon the

assumption that it is anatomically and physiologically impossible for the phloem of the leaves to remove all of the photosynthate as fast as it is formed.

When the supply of sugars entering the sheaths is greater than that which is passing on immediately into the stems, the conditions are ripe for the formation of polysaccharides in the sheaths. Evidence of such a formation occurring in both the April and December experiments has been given in Figs. 1 and 3. In the April experiment, polysaccharides reached a maximum in the sheaths at the time of their minimum concentration in the blades, at 11 p.m. to 3 a.m., indicating that the removal of polysaccharides from the blades by digestion and translocation led to their formation in the sheaths. This was followed by the digestion of polysaccharides and formation of simple sugars in the sheaths, a process necessary for translocation to the stems. Similarly in the December experiment polysaccharides remained high in concentration in the sheaths several hours after they had decreased in the blades, and their sharp decline in the sheaths was accompanied by a marked increase in simple sugars. The evidence indicates that a temporary storage of polysaccharides in the sheaths during the night aids in the translocation of carbohydrates from the blades to the stems.

Another factor affecting translocation is the water content. In the April experiment the sheaths contained more sucrose than simple sugars at every hour tested, whereas in the December experiment the sheaths contained less sucrose than simple sugars. The plants used in the two experiments differed in moisture content. The younger plants taken in December had higher moisture percentages than the older plants taken in April. The lower temperatures and greater amount of cloudiness in December than in April would naturally decrease the rate of water loss from the leaves of the plants taken in December. Differences in age and in the rate of loss of water were probably more important than rainfall in causing the differences in water content, because differences in rainfall were compensated for by irrigation. Therefore it would seem that the immediate cause of the relative amounts of the sugars in the sheaths was the difference in moisture percentage, which in turn was due to the differences in age and season. A similar condition was found in another experiment in plants of the same age which received different supplies of water (12). The sheaths of the plants deprived of water contained more sucrose than simple sugar, whereas the sheaths of the plants supplied with water had more simple sugar then cane sugar. Another experiment not yet published (13) also shows that the factors which increase the moisture percentage favor digestion by invertase rather than synthesis. It is suggested that the relative amounts of the sugars in the sheaths are affected by the amount of water in the sheaths and that the translocation form of sugar predominant in a given plant at a given time is largely dependent upon the content of water.

Without doubt factors other than those just mentioned have important effects upon the process of translocation in the sugar cane plant. The sugar contained in the juices of cane has all originated in the leaf. Studies of the conditions favoring or hindering the translocation of carbohydrates from the leaf to the stalk of sugar cane are essential for an understanding of the fundamentals of sugar production and may lead to an advance in our knowledge of the ripening of cane.

Summary

1. This paper introduces the subject of translocation in the sugar cane plant by a consideration of the nature of the process, the location of its occurrence, the time it takes place, the external and internal factors affecting its speed, and the theories regarding the mechanism of translocation.

2. The results of the analyses of moisture, simple sugars, cane sugar, starch, and total polysaccharides in the sheaths taken at hourly or bi-hourly intervals during the day and the night, are presented in tabular and graphic form.

3. The transport of sugar is shown to occur both day and night.

4. Both cane sugar and the simple sugars are translocated in the sugar cane plant.

5. An important factor determining which form of sugar is translocated the more predominantly in a given plant at a given time is the percentage of water.

6. The temporary storage of polysaccharides in the sheath during the night aids in the translocation of carbohydrates from the blade to the stem.

Acknowledgment

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Further Notes on Water and Cane Ripening

By Constance E. Hartt

The results of a study of the effects of water upon the ripening of sugar cane were reported in 1934 (5). The evidence presented then indicated that some photosynthesis occurred at the wilting point, and that a greater synthesis of sucrose took place in the blades of sugar cane plants supplied with water than in those deprived of water. The first experiment was merely preliminary and the interpretation of the differences was not entirely clear. The study was therefore repeated, and this report touches upon certain aspects of the effect of water upon photosynthesis, translocation, and storage of sugar in the sugar cane plant.

At the suggestion of W. W. G. Moir, the second experiment was expanded to include studies of the enzyme activity in the plants undergoing treatment. Since enzymes are sensitive to external and internal conditions of many kinds, and since other experiments have indicated that they are affected by water content (6), and may thus control the formation of starch and sugar (3, 4), it was hoped that a study of their activity might aid in elucidating the problems of water and cane ripening.

Brief definitions of photosynthesis and of the carbohydrates (8) mentioned in this report, of translocation (9), and of enzymes (7) have been presented in other reports.

Methods

Sugar cane of the variety H 109 was planted in pots of good soil on October 8, 1934, and kept in a sunny part of the grounds of the Experiment Station. The plants were watered and fertilized through the kindness of Dr. A. J. Mangelsdorf, all of the plants receiving optimum water and fertilizer applications until the beginning of the experiment.

The plants were allowed to grow until November 15, 1935, at which time most of the stalks were tasseling. The following series of plants were then inaugurated:

1. Dark wet
2. Dark dry
3. Light wet
4. Light dry
5. Outdoor control

There were 15 pots in each series, the plants in each series being taken from all parts of the plot.

Series 5, the outdoor controls, were left in their original places throughout the experiment, and were watered daily.

On Friday, November 15, 1935, when the plants were 13 months and one week of age, series 1-4 were removed to the greenhouse. Beginning Saturday, November 16, the "dry" plants (series 2 and 4) received no further water, while the "wet" plants (series 1 and 3) were watered daily. By November 20, the "dry" plants

Fig. 1. Sugar cane plants of the variety H 109: at the right, water withheld for five days; at the left, water supplied daily. Photographed the day of removal to the dark.

appeared to be wilting, the leaves being dry, yellow, and somewhat curled at noon. The "wet" plants were in good condition. The appearance of the plants in the greenhouse on November 20 is illustrated in Fig. 1. All of the plants in series 1-4 were placed in the darkened assembly room beginning at 5 p. m. The temperature in the lecture hall was approximately 80-83° F. all of the following day, the heating of the room being conducted with the efficient cooperation of W. Sa Ning. The "light" plants (series 3 and 4) were removed from the darkened assembly room to the greenhouse on the evening of November 21, and received light the following day until 1 p. m., when they were harvested. The "dark" plants remained in the dark until 8 a. m. November 22, when they were harvested. The "outdoor control" plants were harvested at 1 p. m.

The purpose of putting the plants in the dark was to use up their stored carbohydrates. The plants were returned to the light to allow them to conduct photosynthesis.

The following samples were taken in each series, using only tasseling cane:

Blades: Nos. 5, 6, 7, 8 (unless very yellow), midribs included.

Sheaths: Nos. 5, 6, 7, 8.

Green-leaf cane: between attachment of leaf No. 5 and of the lowest living leaf.

Upper dry-leaf cane: the upper half.

Lower dry-leaf cane: the lower half.

Samples were taken for moisture, sugars, and polysaccharides, which were analyzed by our regular methods, the references to which were cited in the former paper (5). The upper and lower dry-leaf cane were sampled for juice analyses, which were conducted by the Sugar Technology Department. The material for the study of enzyme activity was dried with the drying apparatus recently perfected under the direction of Dr. H. L. Lyon, which dries the ground plant material at a temperature between 30 and 40° C.

The enzymes studied in this investigation included invertase, amylase, dextrinase, and maltase. The activity of invertase, the enzyme which aids in the digestion of cane sugar forming simple sugars (glucose and fructose), was determined by measuring the increase in the ability to reduce Soxhlet's solution, when weighed amounts of plant powder (containing the enzyme) were incubated for 24 hours with known quantities of pure sucrose solution as the substrate. The activity of maltase, an enzyme which aids in the digestion of maltose forming glucose, was measured in the same way, using known quantities of pure maltose solution as the substrate. Sucrose does not reduce Soxhlet's solution, so that after a period of incubation any reducing action found is due to the presence of simple sugars, which do reduce Soxhlet's solution. Maltose also reduces Soxhlet's solution, but its reducing action is not as great as that of glucose; hence after a period of incubation any increase in reducing action is due to the presence of glucose. The tests were all performed in duplicate, with suitable controls, and were repeated. The reducing action was determined by the method of Munson and Walker (10). The Bertrand (1) method, titration with potassium permanganate, was used for estimating the amount of copper oxide formed in the Soxhlet's solution. The results are expressed in cubic

centimeters of twentieth normal potassium permanganate, the higher the figure the greater the activity of the enzyme.

The activity of amylase, the enzyme which aids in the digestion of starch forming dextrine, is given as color with iodine-potassium iodide, after incubation for 20 hours at 36.5° C., using soluble starch as the medium. The activity of dextrinase, the enzyme which aids in the digestion of dextrine forming maltose, is given similarly, using dextrine as the medium. The following five colors are used to represent the course of the digestion of starch and dextrine, in the order named: blue, purple, red-purple, dark red, red.

Soil samples for the determination of soil moisture were taken by H. A. Wadsworth, who reported that at the time of the experiment both the "dark dry" and the "light dry" (series 2 and 4) were below the wilting percentage. The wilting percentage, or soil moisture content at which plants wilt, is considered a critical point by Veihmeyer and Hendrickson (13), who found that the leaves of plants below the wilting point had narrower openings of the stomatal pores than the leaves of plants supplied with water; and that no differences in stomatal opening were noticeable in plants above the wilting point even though the soil moisture content fluctuated.

On November 23 the plants were ratooned and irrigation and fertilization started in the usual way. To determine whether or not the drying of the plants affected the development of the ratoons, counts were made of the number of pots which had developed tillers by December 3. The total number of pots which had previously been deprived of water was 28, and all of these contained tillers. The total number of pots which had received water throughout the experiment was 44, but only 40 of these contained tillers on December 3. On December 16 a count was made of the number of tillers per pot, and it was found that the "dry" varied from two to 14, with an average of six, whereas the "wet" varied from one to nine, with an average of five. Evidently the plants previously deprived of water commenced development as well if not better than the plants adequately supplied with water.

The ratoons are now growing and it is planned to repeat the experiment before the development of tassels. It is then hoped to undertake a broader program covering the conditions for ripening for early, intermediate, and late harvest.

Results

The results of the juice analyses are presented in Table I, which shows that the "dark wet" was superior to the "dark dry," and the "light wet" was superior to the "light dry" in the upper dry-leaf cane. In the lower dry-leaf cane, the "dark wet" was superior to the "dark dry," but the "light wet" was not superior to the "light dry."

The results of the moisture determinations are reported in Table II, in which the results are expressed both upon the wet-weight basis and upon the dry-weight basis. These results are disappointing inasmuch as the "dry" series had higher percentages of moisture than the "wet" series, in several places. These results are the moisture percentages of the samples and may not be a true indication of the moisture contents of the plants themselves. In this experiment such large plants and large amounts of material had to be handled that a longer time than usual elapsed between cutting the stalks and weighing the ground samples. In the first

experiment, the "wet" plants had higher percentages of moisture than the "dry" plants in every organ tested.

The percentages of simple sugars are presented in Table III, cane sugar in Table IV, polysaccharides in Table V, and starch in Table VI. The results are expressed in three ways: in percentages upon the wet-weight basis, the dry-weight basis, and the residual dry-weight basis. The last method, which is recommended for experiments of short duration, will be used as the chief basis for discussion in this report. The residual dry weight is the difference between the dry weight and the total sugars plus polysaccharides and is considered to form a more reliable basis for comparison than either the wet-weight basis or the dry-weight basis because it rules out the greater part of the fluctuating compounds.

The results of the carbohydrate analyses in the blades and the sheaths, expressed upon the residual dry-weight basis, are presented in graphic form in Fig. 2, those in the green-leaf cane in Fig. 3, those in the upper dry-leaf cane in Fig. 4, and those in the lower dry-leaf cane in Fig. 5. In Fig. 6 are presented the graphs of the total sugars plus polysaccharides, which may be taken to represent the total metabolizable carbohydrate material. The possible relationships of these results will be considered in the discussion.

The activity of invertase, determined without additional buffers and at pH 4.5 using the buffers of McIlvaine (2), is reported in Table VII. The results of the determinations of maltase activity are presented in Table VIII, and those of amylase and dextrinase in Table IX.

TABLE I

Juice Analyses

Series	Brix	Pol.	Sucrose	Apparent Purity	Gravity Purity	Glucose	Q.R.
			Upper dry-leaf cane				
1—dark wet	18.07	14.88	15.34	82.35	84.89	1.51	9.34
2—dark dry	17.54	14.25	14.72	81.24	83.92	1.58	9.85
3—light wet	18.23	15.34	15.80	84.15	86.73	1.33	8.93
4—light dry	17.83	14.47	14.98	81.16	84.02	1.60	9.71
5—outdoor control	18.42	14.81	15.34	80.40	83.28	1.67	9.55
			Lower dry-leaf cane				
1—dark wet	20.27	19.19	19.45	94.67	95.95	0.15	6.64
2—dark dry	19.82	18.60	18.81	93.84	94.90	0.23	6.88
3—light wet	20.02	18.60	18.91	92.91	94.46	0.26	6.92
4—light dry	19.87	18.73	18.94	94.26	95.32	0.13	6.82
5—outdoor control	20.50	19.04	19.37	92.88	94.49	0.28	6.76

TABLE II

Moisture Determinations

Series	Blades	Sheaths	Green cane	Upper dry	Lower dry
	Percentages expressed on wet-weight basis				
1—dark wet	64.75±0.029	66.18	79.09±0.009	73.07±0.038	66.93±0.024
2—dark dry	65.61±0.048	68.08±0.019	79.30±0.052	74.12±0.019	68.59±0.052
3—light wet	64.25±0.086	69.60±0.286	77.51±0.186	70.77±0.172	70.06±0.062
4—light dry	63.88±0.176	65.70	78.84±0.114	73.57±0.133	69.99±0.024
5—outdoor control	65.06±0.048	69.95±0.229	78.45±0.014	72.20±0.162	68.41±0.114
	Percentages expressed on dry-weight basis				
1—dark wet	183.7±0.238	195.7	378.3±0.191	271.3±0.525	202.4±0.238
2—dark dry	190.8±0.382	213.3±0.191	383.1±1.240	286.4±0.286	218.4±0.525
3—light wet	179.7±0.668	229.1±3.100	344.9±3.673	242.1±2.003	234.0±0.715
4—light dry	176.9±1.384	191.5	372.7±2.576	278.4±1.908	233.2±0.238
5—outdoor control	186.2±0.382	232.8±2.528	349.3±7.441	259.8±2.146	216.5±1.097

TABLE III

Simple sugars; percentages expressed on the wet-weight basis, the dry-weight basis and the residual dry-weight basis.

Series	Wet weight	Dry weight	Residual dry weight
Blades:			
1—dark wet	0.200±0.006	0.566±0.016	0.790±0.021
2—dark dry	0.437±0.017	1.273±0.051	1.814±0.077
3—light wet	0.316±0.000	0.884±0.001	1.297±0.002
4—light dry	0.550±0.001	1.525±0.001	2.199±0.006
5—outdoor control	0.339±0.001	0.972±0.005	1.410±0.007
Sheaths:			
1—dark wet	0.696±0.001	2.059±0.004	2.978±0.008
2—dark dry	0.822±0.007	2.577±0.023	3.741±0.042
3—light wet	0.740±0.001	2.435±0.003	3.679±0.015
4—light dry	0.855±0.004	2.495±0.013	3.720±0.011
5—outdoor control	0.860±0.005	2.864±0.004	4.361
Green-leaf cane:			
1—dark wet	2.157±0.016	10.321±0.079	28.912±0.241
2—dark dry	2.064±0.007	9.972±0.032	27.808±0.128
3—light wet	1.948±0.006	8.664±0.028	22.987±0.138
4—light dry	2.389±0.002	11.292±0.011	33.104
5—outdoor control	1.976±0.004	9.233±0.013	25.730
Upper dry-leaf cane:			
1—dark wet	1.421±0.003	5.276±0.012	17.301±0.168
2—dark dry	1.475±0.008	5.701±0.029	23.109±0.178
3—light wet	0.679±0.010	2.324±0.034	7.440±0.101
4—light dry	1.122±0.017	4.249±0.066	16.329±0.213
5—outdoor control	1.131±0.005	4.069±0.019	13.144±0.054
Lower dry-leaf cane:			
1—dark wet	0.404±0.007	1.223±0.021	3.787±0.085
2—dark dry	0.272±0.002	0.867±0.008	3.195±0.010
3—light wet	0.328±0.002	1.097±0.007	3.952±0.026
4—light dry	0.279±0.002	0.932±0.004	3.478±0.012
5—outdoor control	0.334±0.005	1.059±0.015	3.060±0.028

TABLE IV

Cane sugar; percentages expressed on the wet-weight basis, the dry-weight basis, and the residual dry-weight basis.

Series	Wet weight	Dry weight	Residual dry weight
Blades:			
1—dark wet	0.509±0.002	1.447±0.019	2.016±0.023
2—dark dry	0.585±0.019	1.700±0.054	2.421±0.083
3—light wet	1.435±0.011	4.016±0.032	5.894±0.049
4—light dry	1.071±0.004	2.966±0.025	4.275±0.019
5—outdoor control	1.225±0.022	3.506±0.062	5.085±0.088
Sheaths:			
1—dark wet	1.412±0.039	4.176±0.115	6.039±0.169
2—dark dry	1.226±0.010	3.840±0.033	5.573±0.062
3—light wet	1.373±0.006	4.516±0.020	6.823±0.066
4—light dry	1.456±0.003	4.245±0.008	6.328±0.000
5—outdoor control	2.087±0.011	6.946±0.039	10.313
Green-leaf cane:			
1—dark wet	6.772±0.036	32.383±0.182	90.707±0.574
2—dark dry	6.388±0.026	30.861±0.125	86.057±0.471
3—light wet	6.463±0.001	28.735±0.004	76.223±0.225
4—light dry	6.443±0.020	30.449±0.094	89.646
5—outdoor control	7.438±0.007	34.457±0.003	103.93
Upper dry-leaf cane:			
1—dark wet	11.646±0.045	43.298±0.190	141.813±1.594
2—dark dry	11.457±0.034	44.271±0.131	176.831±1.782
3—light wet	12.224±0.046	41.822±0.158	133.859±0.668
4—light dry	11.787±0.025	44.598±0.096	171.395±0.788
5—outdoor control	11.150±0.078	40.110±0.283	129.621±2.066
Lower dry-leaf cane:			
1—dark wet	14.214±0.031	42.985±0.097	132.977±0.322
2—dark dry	14.730±0.043	46.898±0.139	172.770±1.429
3—light wet	14.254±0.013	47.608±0.045	171.347±0.174
4—light dry	14.570±0.065	48.550±0.216	181.152±1.920
5—outdoor control	13.393±0.115	42.395±0.364	122.519±1.635

TABLE V

Polysaccharides; percentages expressed on the wet-weight basis, the dry-weight basis, and the residual dry-weight basis.

Series	Wet weight	Dry weight	Residual dry weight
Blades:			
1—dark wet	9.14±0.095	25.96±0.277	36.21±0.439
2—dark dry	9.20±0.024	26.77±0.062	38.14±0.195
3—light wet	9.62±0.005	26.95±0.019	39.57±0.029
4—light dry	9.43±0.105	26.14±0.300	37.72±0.587
5—outdoor control	9.29±0.029	26.59±0.086	38.61±0.133
Sheaths:			
1—dark wet	8.31±0.029	24.61±0.086	35.61±0.100
2—dark dry	7.88±0.038	24.68±0.119	35.84±0.257
3—light wet	8.15±0.100	26.84±0.334	40.59±0.725
4—light dry	8.93±0.048	26.18±0.148	39.05±0.296
5—outdoor control	7.12	23.67	35.59
Green-leaf cane:			
1—dark wet	4.51±0.048	21.59±0.234	60.56±0.620
2—dark dry	4.82±0.019	23.30±0.105	65.09±0.215
3—light wet	5.59±0.014	24.90±0.071	66.15±0.405
4—light dry	5.05	23.85	69.94
5—outdoor control	4.43	20.57	57.61
Upper dry-leaf cane:			
1—dark wet	6.81±0.038	25.28±0.148	83.06±1.078
2—dark dry	6.56±0.024	25.35±0.095	102.85±0.095
3—light wet	7.19±0.024	24.61±0.086	78.87±0.153
4—light dry	6.65±0.009	25.13±0.033	96.84±0.396
5—outdoor control	6.91±0.000	24.90±0.009	80.62±0.706
Lower dry-leaf cane:			
1—dark wet	7.77±0.076	23.46±0.224	72.66±1.021
2—dark dry	7.89±0.005	25.08±0.009	92.57±0.534
3—light wet	7.04±0.009	23.51±0.033	84.87±0.119
4—light dry	7.12±0.014	23.71±0.043	88.64±0.391
5—outdoor control	6.94±0.057	21.93±0.181	63.48±0.224

TABLE VI

Starch; percentages expressed on the wet-weight basis, the dry-weight basis, and the residual dry-weight basis.

Series	Wet weight	Dry weight	Residual dry weight
Blades:			
1—dark wet	0.188±0.022	0.534±0.062	0.745±0.088
2—dark dry	0.080±0.019	0.235±0.055	0.335±0.079
3—light wet	0.181±0.009	0.508±0.025	0.745±0.037
4—light dry	0.058±0.005	0.161±0.013	0.232±0.020
5—outdoor control	0.128±0.003	0.367±0.008	0.533±0.012
Sheaths:			
1—dark wet	0.055±0.005	0.165±0.016	0.239±0.024
2—dark dry	0.066±0.000	0.207±0.001	0.301±0.001
3—light wet	0.073±0.006	0.240±0.019	0.363±0.031
4—light dry	0.060±0.005	0.177±0.015	0.264±0.023
5—outdoor control	0.038±0.002	0.130±0.007	0.172
Green-leaf cane:			
1—dark wet	0.659	3.154	8.859
2—dark dry	0.462±0.000	2.233±0.004	6.238±0.003
3—light wet	0.481±0.010	2.141±0.048	5.689±0.145
4—light dry	0.408	1.927	5.651
5—outdoor control	0.677±0.017	3.145±0.088	8.294
Upper dry-leaf cane:			
1—dark wet	0.913±0.010	3.390±0.038	11.139±0.202
2—dark dry	0.841±0.033	3.249±0.129	13.189±0.563
3—light wet	1.242±0.016	4.248±0.054	13.615±0.153
4—light dry	1.112±0.044	4.204±0.167	16.194±0.599
5—outdoor control	1.289±0.021	4.642±0.075	15.019±0.104
Lower dry-leaf cane:			
1—dark wet	1.238±0.023	3.740±0.071	11.577±0.168
2—dark dry	1.031±0.002	3.280±0.010	12.105±0.026
3—light wet	0.963±0.034	3.153±0.083	11.384±0.302
4—light dry	0.949±0.044	3.162±0.146	11.839±0.620
5—outdoor control	1.383±0.001	4.371±0.004	12.652±0.073

TABLE VII

Invertase activity expressed in cc. N/20 $KMnO_4$.

Series	Blades	Sheaths	Green cane	Upper dry	Lower dry
		Activity Unbuffered			
1—dark wet	6.92	10.56	3.61	1.67	1.42
2—dark dry	7.64	9.94	6.70	1.45	1.09
3—light wet	9.08	10.33	6.07	1.33	0.67
4—light dry	6.71	12.95	6.06	2.35	0.58
5—outdoor control	17.34	14.92	5.92	2.57	2.01
		Activity at pH 4.5.			
1—dark wet	10.65	15.90	5.15	2.07	1.48
2—dark dry	12.22	15.19	5.97	2.22	1.78
3—light wet	15.48	18.05	5.83	1.14	1.66
4—light dry	12.10	18.94	5.70	2.36	1.44
5—outdoor control	20.72	17.02	5.11	2.34	2.74

TABLE VIII

Maltase activity expressed in cc. N/20 $KMnO_4$.

Series	Blades	Sheaths	Green cane	Upper dry	Lower dry
		Activity Unbuffered			
1—dark wet	3.35	5.21	7.96	4.51	4.07
2—dark dry	3.81	3.95	13.36	3.61	2.53
3—light wet	6.44	5.11	12.61	4.72	3.56
4—light dry	4.16	3.62	14.57	5.27	2.18
5—outdoor control	4.11	4.86	11.78	6.61	6.46
		Activity at pH 4.5.			
1—dark wet	3.72	5.25	7.49	6.20	5.15
2—dark dry	5.42	3.87	7.60	7.01	4.72
3—light wet	6.47	3.47	7.64	3.50	3.55
4—light dry	4.40	2.71	9.02	6.90	4.07
5—outdoor control	4.30	3.49	7.60	7.55	5.92

TABLE IX

Amylase and dextrinase activity, expressed as color when tested with iodine.

Series	Amylase	Dextrinase
Blades:		
1—dark wet	dark red	dark red
2—dark dry	red-purple	red-purple
3—light wet	red	dark red
4—light dry	red-purple	red-purple
5—outdoor control	red	dark red
Sheaths:		
1—dark wet	purple	red-purple
2—dark dry	purple	red-purple
3—light wet	purple	red-purple
4—light dry	purple	red-purple
5—outdoor control	purple	red-purple
Green-leaf cane:		
1—dark wet	blue	purple
2—dark dry	blue	purple
3—light wet	blue	purple
4—light dry	blue	purple
5—outdoor control	blue	purple
Upper dry-leaf cane:		
1—dark wet	blue	purple
2—dark dry	blue	purple
3—light wet	blue	purple
4—light dry	blue	purple
5—outdoor control	blue	purple
Lower dry-leaf cane:		
1—dark wet	blue	purple
2—dark dry	blue	purple
3—light wet	blue	purple
4—light dry	blue	purple
5—outdoor control	blue	purple

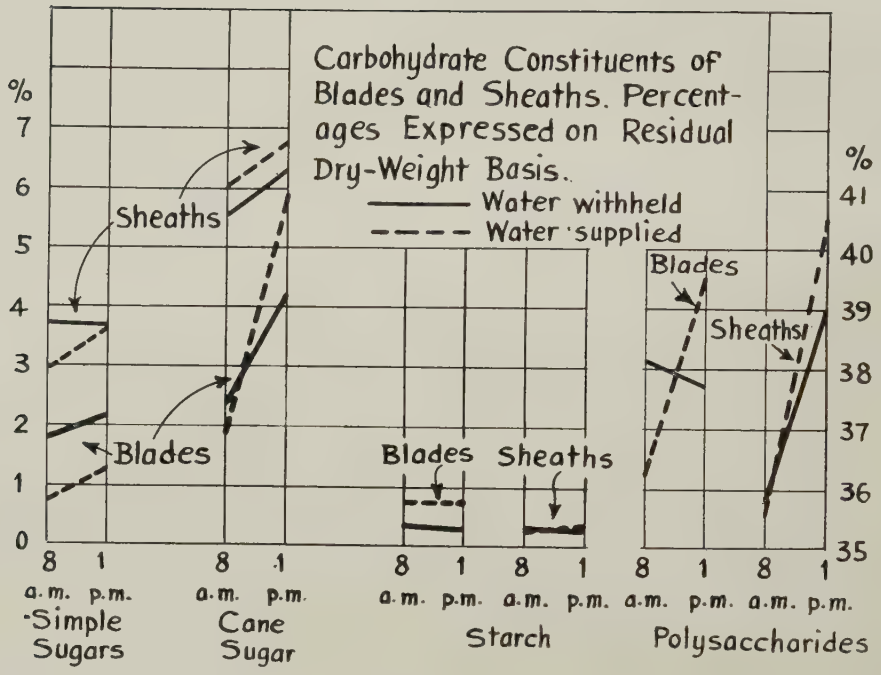
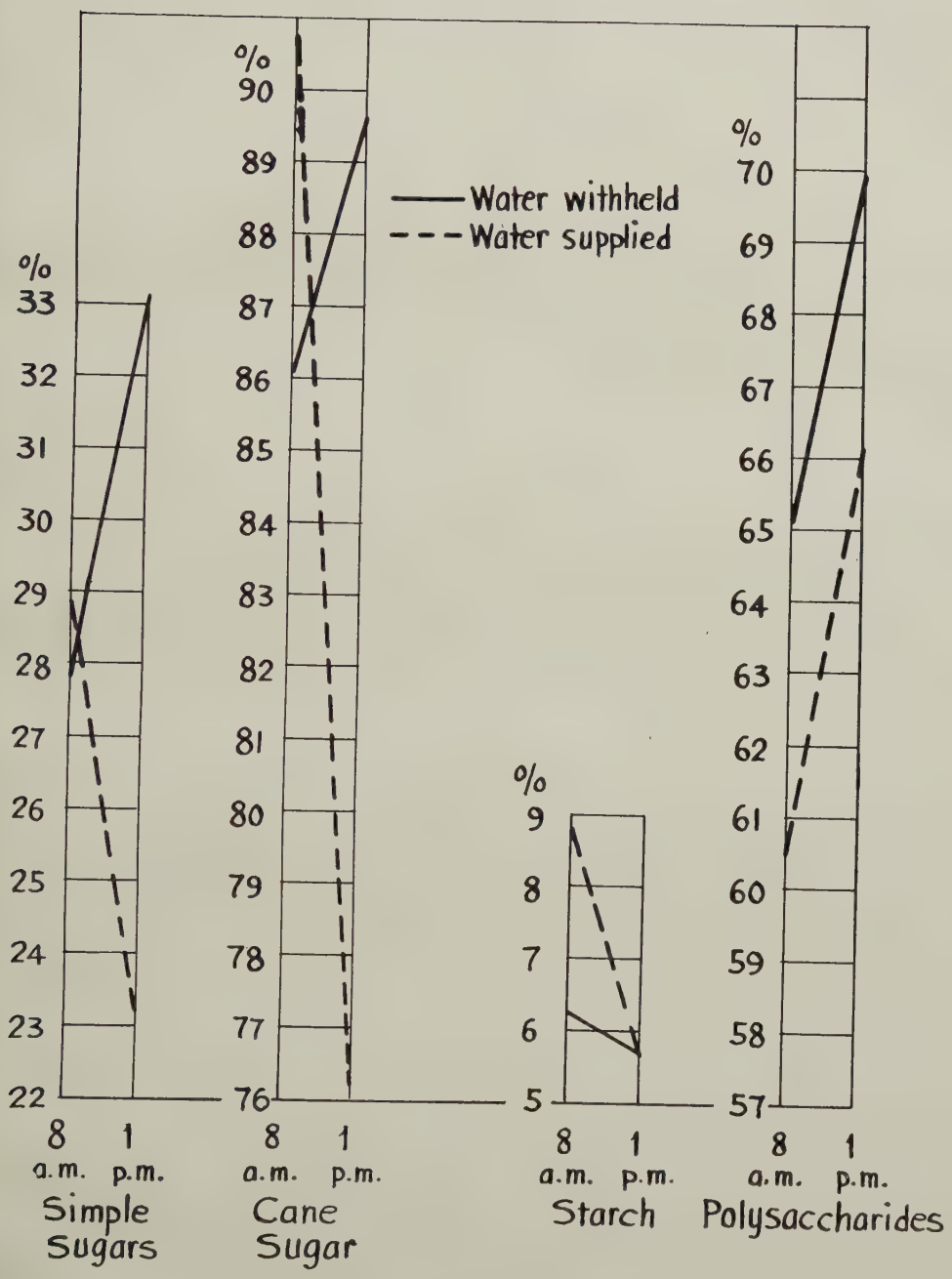

Carbohydrate Constituents of Blades and Sheaths. Percentages Expressed on Residual Dry-Weight Basis.
Water withheld
Water supplied
%
7
6
5
4
3
2
1
0
%
41
40
39
38
37
36
35
Sheaths
Blades
Blades
Sheaths
Blades
Sheaths
8 1 8 1 8 1 8 1 8 1 8 1 8 1 8 1
a.m. p.m. a.m. p.m. a.m. p.m. a.m. p.m. a.m. p.m. a.m. p.m. a.m. p.m.
Simple Sugars
Cane Sugar
Starch
Polysaccharides

Fig. 2.


Carbohydrate Constituents of Green-Leaf Cane.
Percentages Expressed on Residual Dry-Weight Basis.
Water withheld
Water supplied
%
33
32
31
30
29
28
27
26
25
24
23
22
%
90
89
88
87
86
85
84
83
82
81
80
79
78
77
76
%
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8
7
6
5
%
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68
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66
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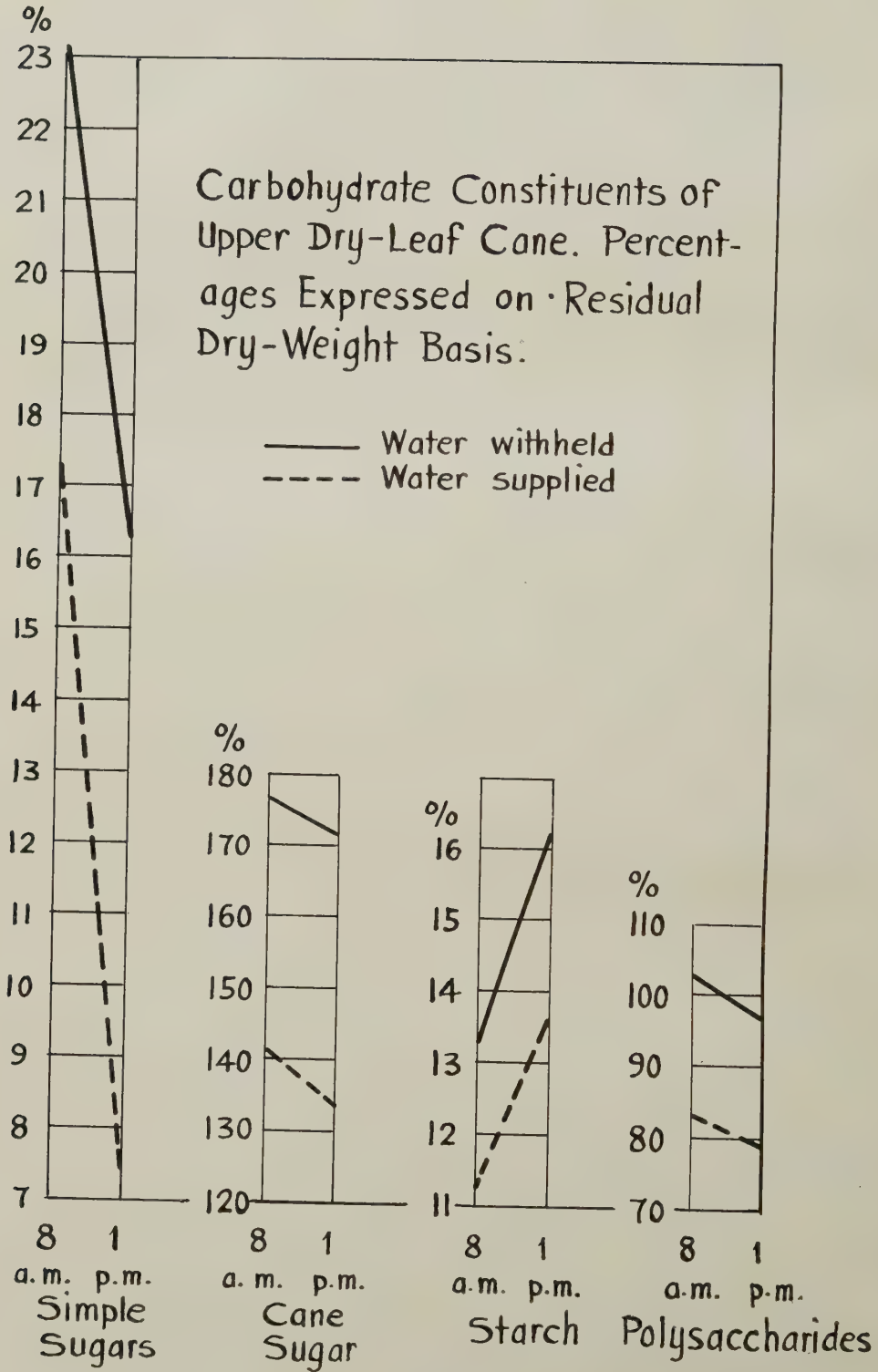
8 1
a.m. p.m.
Simple Sugars
Cane Sugar
Starch
Polysaccharides

Fig. 3.


%
23
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8
7
Carbohydrate Constituents of Upper Dry-Leaf Cane. Percentages Expressed on Residual Dry-Weight Basis.
Water withheld
Water supplied
8 1
a.m. p.m.
Simple Sugars
%
180
170
160
150
140
130
120
Cane Sugar
%
16
15
14
13
12
11
Starch
%
110
100
90
80
70
Polysaccharides

Fig. 4.

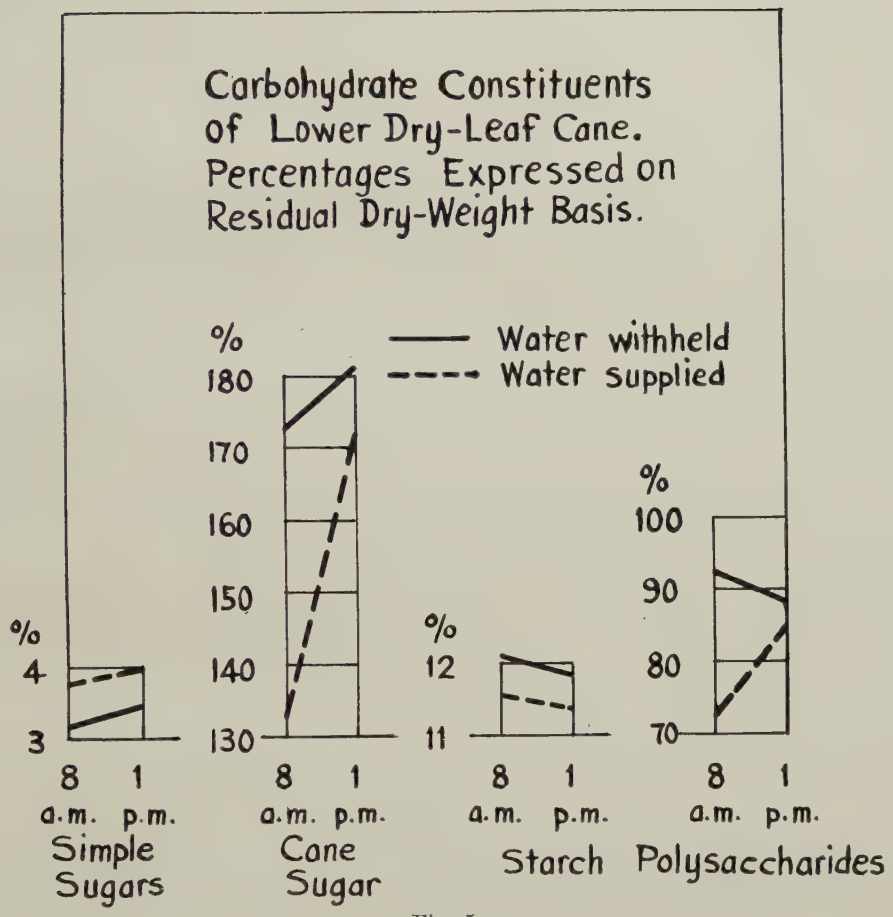
Carbohydrate Constituents
of Lower Dry-Leaf Cane.
Percentages Expressed on
Residual Dry-Weight Basis.
Water withheld
Water supplied
%
4
3
%
180
170
160
150
140
130
%
12
11
%
100
90
80
70
8 1
a.m. p.m.
Simple Sugars
Cane Sugar
Starch
Polysaccharides

Fig. 5.

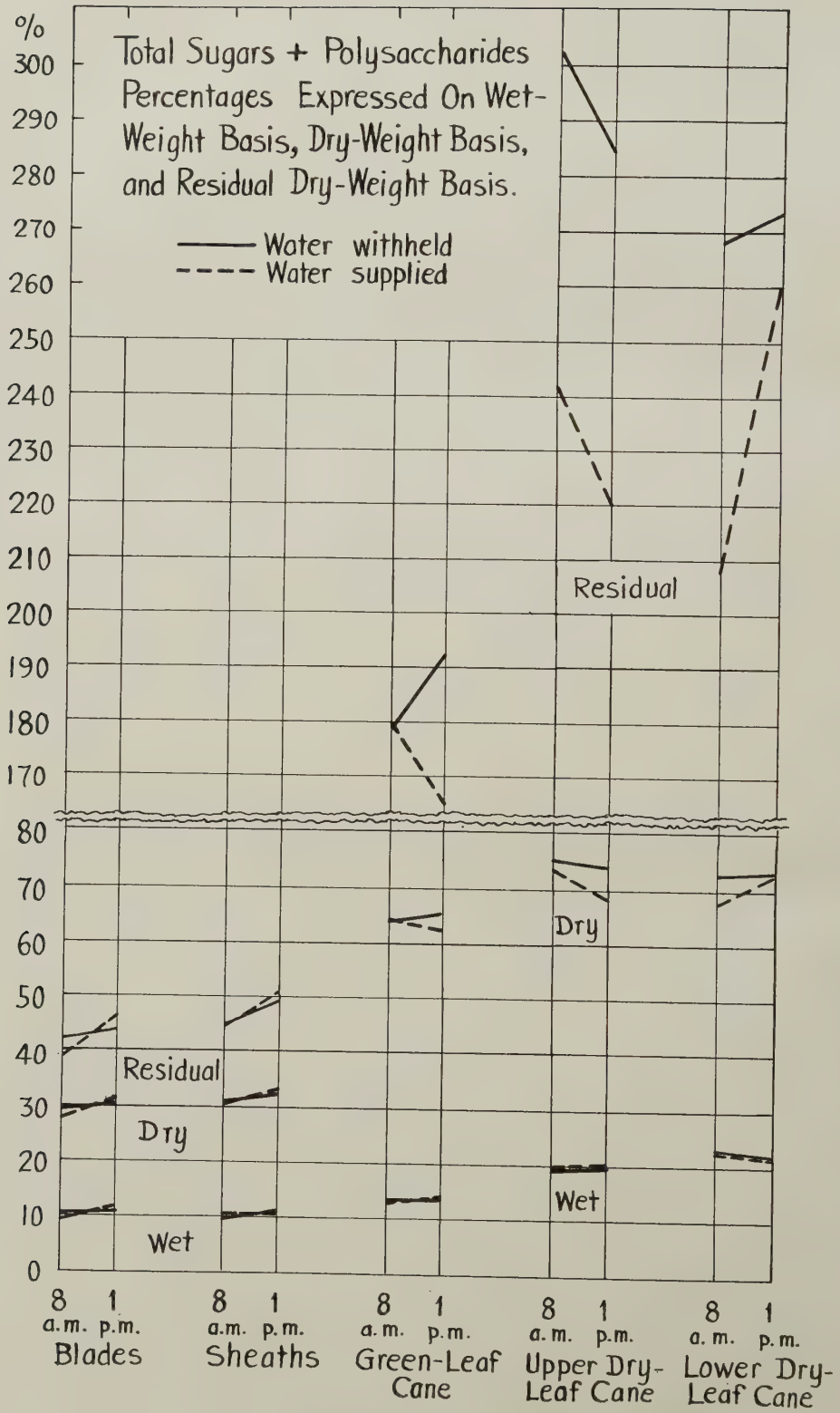
%
300
290
280
270
260
250
240
230
220
210
200
190
180
170
80
70
60
50
40
30
20
10
0
Total Sugars + Polysaccharides
Percentages Expressed On Wet-
Weight Basis, Dry-Weight Basis,
and Residual Dry-Weight Basis.
Water withheld
Water supplied
Residual
Dry
Wet
Residual
Dry
Wet
8 a.m.
1 p.m.
Blades
Sheaths
Green-Leaf Cane
Upper Dry-Leaf Cane
Lower Dry-Leaf Cane

Fig. 6.

Discussion

Simple Sugars:

The fluctuations in the simple or reducing sugars (glucose and fructose) are in the same direction on the three bases of calculation with the exception of the lower dry-leaf cane, in which the plants supplied with water decreased slightly during exposure to light when calculated upon the wet and dry bases but increased a trifle when calculated upon the residual dry-weight basis. The differences are accentuated upon the residual basis, and from these results the following observations are recorded:

In the blades, the content of simple sugars increased during exposure to light, in both series of plants, with a greater increase in the plants supplied with water than in those deprived of water. Thus although the manufacture of simple sugars may take place in the blades of plants below the wilting point, yet the process proceeds better in plants receiving an adequate supply of water.

In the sheaths there was an increase in simple sugars in the plants supplied with water but not in the others. It may be either that the favorable water supply increased the production of simple sugars in the sheaths, or that the sheaths of the plants supplied with water received more simple sugars from the blades, because the blades were able to manufacture more simple sugars.

In the green-leaf cane, there was a decrease in the percentage of simple sugars in the plants receiving water, but an increase in the plants deprived of water. These differences seem best explained, at least in part, by utilization in growth and respiration in the plants receiving water and a curtailment of such utilization in the plants deprived of water. It is assumed that some of the sugar was being used in the formation of tassels, and that such a use would take place more readily in the plants supplied with water than in the plants from which water was withheld.

In the upper dry-leaf cane, the simple sugars decreased in both series, while in the lower dry-leaf cane there was a small increase in both series. At present no explanation of these differences is offered.

Cane Sugar:

The results by the three bases of calculation do not always show the same tendencies. The tendencies are the same in the blades and sheaths but different in the stems. The results expressed upon the dry-weight and the residual dry-weight bases agree except in the upper dry-leaf cane, in which no change was indicated in the plants deprived of water, on the dry-weight basis, but on the residual dry-weight basis those plants show a decrease in sucrose. The results on the wet-weight basis show more nearly uniform sucrose content than on the other bases of computation.

Using the residual dry-weight basis of calculation, the following observations may be made:

In the blades, there was an increase in the percentage of sucrose during exposure to light with a greater increase in the plants supplied with water than in the others. Therefore sucrose may be made in the blades of plants which are below the wilting point, but more sucrose is made when the supply of water is adequate. This conclusion agrees with that for simple sugars.

In the sheaths, the sucrose content was a little higher in the plants receiving water than in the others. There was a small increase in both series during the period of illumination. Evidently a little more cane sugar was translocated into the sheaths of the plants receiving water, probably because of the better manufacture of sucrose in the blades of the same plants.

In the green-leaf cane, the plants receiving water decreased in the percentage of sucrose, probably partly due to digestion and utilization in growth and respiration, but also due to translocation as indicated by the considerable increase in the percentage of sucrose in the lower dry-leaf cane of the same plants.

The plants deprived of water surpassed the others in sucrose content in the green-leaf cane. They also contained higher percentages of sucrose in both parts of the dry-leaf cane. Inasmuch as these plants were receiving the same supply of water as the others when the dry-leaf cane was being formed, it is apparent that these differences in sucrose content were not caused by differences in water content during growth. Perhaps the smaller amount of sucrose translocated from the blades into the green-leaf cane of the plants deprived of water, accumulated there due to lack of utilization; whereas in the plants supplied with water so much sucrose was used by further translocation, growth, and respiration that the result was a decrease during the period of illumination. Similarly, in the dry-leaf cane, little sucrose was used in the plants deprived of water, so that the sucrose content remained high during the experiment.

If we explain the lower general level of cane sugar in the dry-leaf cane of the plants supplied with water by assuming greater utilization of the sugar, one may question the possibility of explaining the greater increase in the percentage of cane sugar in the plants receiving water as due to better translocation. Both explanations seem justifiable, however, since the increase due to better translocation occurred during exposure to light, and the decrease due to greater utilization probably occurred during the period of darkness, inasmuch as the sugar content was already low at 8 a. m., the time of the first sampling. In other words, while the plants were in the dark, those receiving water lost more sucrose in their dry-leaf cane than the others, and after they were returned to the light the plants supplied with water were able to translocate more sucrose to their dry-leaf cane because of their greater manufacture of sugar in the blades and perhaps also because of a greater rate of translocation. The plants receiving water are thus assumed to have had a greater rate of metabolism than the plants deprived of water.

Starch:

The starch content of the blades and sheaths was so low that its presence is questionable. The blades of the plants supplied with water appeared to contain more starch than the blades of the other plants. There is no evidence of the formation of starch in the blades of either series of plants during the period of illumination. Neither is there any evidence in this study of a conversion of starch or of polysaccharides as a whole into sucrose, in the plants below the wilting point, as has been suggested by others workers (3, 4, 12).

In the green-leaf cane, starch decreased during exposure to light, and this decrease was the greater in the plants receiving water, another evidence of their greater metabolic rate.

In the upper dry-leaf cane starch increased during the period of illumination, and in the lower dry-leaf cane there was a small decrease in both series. The plants deprived of water contained more starch than the other plants, in both the upper and lower dry-leaf cane.

Polysaccharides:

In the blades, there was an increase in the percentage of polysaccharides in the plants supplied with water, but in the other plants the differences were insignificant. Thus photosynthesis and subsequent processes resulted in the formation of polysaccharides only in the plants adequately supplied with water. The blades of the plants deprived of water could conduct enough photosynthesis to form simple sugars and sucrose, but not enough to form starch and other polysaccharides.

That the blades of the plants receiving water produced polysaccharides other than starch is shown by the greater percentages of polysaccharides than of starch and by the increase in polysaccharides during exposure to light, which was unaccompanied by an increase in starch. The nature of these other polysaccharides would form another study.

In the sheaths, there was an accumulation of polysaccharides in both series, with the greater accumulation in the plants supplied with water. That the sheaths of the plants deprived of water accumulated polysaccharides at all is of interest, since the blades of the same plants did not, and is another indication of the lower metabolic rate of those plants, i. e., they may have respired little so there was a surplus of sugar to be stored as polysaccharides in the sheaths, even though none was formed in the blades.

In the green-leaf cane the percentage of polysaccharides increased in both series during exposure to light. The plants deprived of water surpassed the others at both sampling hours, indicating less utilization of carbohydrates by the former.

In the upper and lower dry-leaf cane of both series, there were small changes in the percentage of polysaccharides, which may have no important physiological basis. It is of interest that the plants deprived of water surpassed the others in polysaccharide content, agreeing with the polysaccharide content of the green-leaf cane and with sucrose and starch in the dry-leaf cane.

Total Sugars Plus Polysaccharides:

The paragraphs dealing with simple sugars, cane sugar, starch, and polysaccharides all indicate the same thing, viz: (1) that although photosynthesis can take place in plants below the wilting point, yet there is more photosynthesis in plants which are adequately supplied with water; that (2) translocation of carbohydrates takes place better in the plants receiving water; but that (3) due to a curtailment in utilization, the storage of carbohydrates is greater in the plants deprived of water.

A summation of the differences in the carbohydrate constituents determined in our study may be obtained by adding the percentages of total sugars and the per-

centages of polysaccharides. The results of this addition are plotted in Fig. 6, using all three of the bases of calculation. This category may be considered to represent the total metabolizable carbohydrate. The sum of the total sugars plus polysaccharides in the blades is an indication of the amount of photosynthate, but it is not a complete figure because some of the photosynthate is translocated immediately and some is used in forming fats, proteins, and other compounds, and some is respired.

In all comparisons, differences on the wet-weight basis are very small, this leveling probably being due to the presence of several factors fluctuating in different directions, some increasing while others decrease. The residual dry-weight basis is considered the most reliable, because it eliminates the fluctuations in water and in carbohydrates, which are the greatest items in fluctuation. In every comparison, the results on the dry-weight basis agree with those on the residual dry-weight basis, the differences being intensified on the latter basis. The following conclusions may be drawn from the results using the dry-weight and residual dry-weight bases:

(1) The synthesis of carbohydrates takes place in the blades of plants which have been kept a few days at a soil moisture content at or below the wilting point. However, the synthesis is greater in the blades of plants adequately supplied with water.

(2) Translocation of carbohydrates into the sheaths takes place in plants at or below the wilting point, but there is more translocation in the plants supplied with water probably because there is a greater source of supply of carbohydrates in the blades of the plants supplied with water.

(3) The carbohydrate content of the stem of the sugar cane plant does not remain equal during the day, there being changes both in the green-leaf cane and in the dry-leaf cane.

(4) In the green-leaf cane, an adequate water supply caused a decrease in carbohydrates, which might be due to greater utilization in growth or better translocation, or both. A similar decrease with similar possible explanations, occurred in the upper part of the dry-leaf cane. None would be used in growth there but it would be used in respiration. Evidence that much of the decrease in carbohydrate in the green-leaf cane and upper dry-leaf cane was due to translocation is indicated by the increase in carbohydrate in the lower dry-leaf cane, which was greater in the plants supplied with water than in those deprived of water. This increase could not be due to photosynthesis. Neither could it be due to condensation alone, as it is an increase in total metabolizable carbohydrate and not in just the higher forms. Therefore this increase represents a supply coming into the lower dry-leaf cane from above.

(5) In the green-leaf cane, the plants deprived of water increased in total metabolizable carbohydrate after they were exposed to the light. The plants from which water was withheld surpassed the others in total metabolizable carbohydrate, not only in the green-leaf cane but also in both parts of the dry-leaf cane. This difference is not due to the growth conditions of the plants, as they all received adequate water while the dry-leaf cane was being formed. The presence of more total metabolizable carbohydrate in the stems of the plants deprived of water than in the others, is a recent difference and is probably due to less utilization during the period of darkness.

Which is the Better Plant?

The plants receiving water were superior in photosynthesis and translocation.

The plants deprived of water were superior in the storage or conservation of carbohydrates in the stem.

If all of the cane sugar present in the stem could be extracted in the mills, then the plants deprived of water are the better from an economic standpoint. Table I, however, shows that the plants receiving water had better juices than the other plants, with one exception. Evidently the sugar present in the plants receiving water was more readily expressed than that in the plants deprived of water.

Comparison of the Two Experiments:

Because the experiment herein reported is the second in a series of studies of water and cane ripening, a comparison of the results of the two tests may be of interest.

The conditions of the experiments differed in several ways. In the first study, the variety D 1135 was used, whereas in the second study the variety H 109 was used. The plants used in the first study were 12 months of age and were not tasseling; those in the second study were 13 months of age and were all tasseling. In the first test the plants had not received uniform treatment prior to the beginning of the experiment, whereas in the second test all of the plants received uniform treatment until the start of the differential treatments. In the first test no analyses could be made of the dry-leaf cane, whereas in the second test analyses of both the upper and lower dry-leaf cane were included.

The results of the moisture determinations were more satisfactory in the first test, inasmuch as in every instance the plants supplied with water contained higher percentages of moisture than the plants deprived of water. In the second test the moisture relationships were irregular, probably because a longer time than usual elapsed between cutting the stalks and weighing the ground samples, due to the unusually large amount of material to be handled.

The plants used in the second test had consistently lower percentages of moisture than the plants of the first test. In the first test, the sheaths of the plants supplied with water had higher percentages of simple sugars than of cane sugar, and the sheaths of the plants deprived of water had lower percentages of simple sugars than of cane sugar. The possibility that the relative amounts of these two forms of sugars are dependent upon the percentage of water has also been indicated in other work (9). In the experiment herein reported the percentages of cane sugar were always higher than the percentages of simple sugars, in every organ, which may be due in part to the consistently lower percentages of moisture in the second experiment.

The trends in some of the carbohydrate constituents differed in the two experiments, in some organs. It would seem, however, that these differences in trends are of minor importance, inasmuch as the data obtained in the two studies lead to similar conclusions. The conclusions of the first experiment are confirmed and amplified by the results of the second experiment.

Both experiments show that photosynthesis may take place at or below the wilting point. In the first test, the blades of the plants deprived of water increased in simple sugars, cane sugar, and polysaccharides, when exposed to sunlight for seven hours after a period of 45 hours in absolute darkness. In the second test, the blades of the plants deprived of water increased in simple sugars and cane sugar but not in polysaccharides.

Both experiments show that photosynthesis takes place better in plants supplied with water than in plants at or below the wilting point. The evidence in the first test consisted in a greater formation of sucrose in the blades of the plants supplied with water than in the others. The evidence in the second test consisted in greater formation of simple sugars and of cane sugar and, in addition, in a formation of polysaccharides in the blades of the plants supplied with water.

In the first test, the explanation of the differences in simple sugars, cane sugar, and polysaccharides in the sheaths and stems could not be definitely determined, because the data were incomplete; it was merely stated that the differences could be explained by assuming either greater utilization of food by the plants supplied with water during seven hours' exposure to light or better translocation in the same plants. The results of the second test, in which more complete data were obtained, indicate that both of these assumptions are required for an adequate explanation. The evidence for this statement is discussed in the sections headed *Cane Sugar* and *Total Sugars plus Polysaccharides.*

Enzyme Activity in Blades:

Table VII shows that the activity of invertase was greater in series 5 (outdoor controls) than in any of the treated series, whether tested without the addition of buffers or buffered at pH 4.5. Because all of the treated plants were held in the dark for a period of 48 hours, but only half of the plants were deprived of water, it is evident that the decrease in the activity of invertase was a result of the lack of illumination rather than the deprivation of water. Therefore a period of 48 hours in total darkness results in a decrease in the activity of invertase.

In the dark, the activity of invertase was slightly greater in the plants deprived of water than in those supplied with water, whereas in the light the "wet" plants had more active invertase than the "dry" plants. This may indicate that of the plants harvested in the dark, those supplied with water were harmed more in their invertase activity than were those deprived of water; and that of those returned to the light, the plants receiving water increased in their invertase activity while the others did not. Therefore invertase is more responsive to changes in light and darkness when there is plenty of water than when the water supply is deficient. In other words, the activation of invertase in the light and its inactivation in darkness are processes which are favored by a plentiful supply of water. The nature of these changes is not known; they may either be chemical or changes in the colloidal dispersion of the enzyme. The decrease in the dark might be positive adsorption and the increase in the light might be negative adsorption.

Table VIII shows that the most active maltase was found in series 3 (light wet). The activity of maltase in the outdoor control was intermediate, thus differing from invertase, in which the outdoor control was the most active. The 48-hour period of

darkness may have resulted in a slight decrease in maltase in the plants supplied with water, but none was indicated in those deprived of water.

This experiment shows that maltase is less sensitive to darkness than is invertase. Both enzymes when in the dark showed slightly greater activity in the plants deprived of water, and when in the light showed the greater activity in the plants supplied with water.

Table IX shows that of the treated blades, series 3 (light wet) had the most active amylase, which was equal to that of the outdoor control. Withholding water resulted in a decrease in the activity of amylase. Amylase activity in the plants plentifully supplied with water was decreased by darkness; but there is no evidence of a harmful effect of darkness upon the amylase of the plants deprived of water.

Table IX shows greater dextrinase activity in the plants supplied with water than in those deprived of water, both in the dark and the light. There was no evidence of an effect of light upon the activity of dextrinase.

It is interesting that of all the treated blades, series 3 (light wet) had the most active amylase, maltase, and invertase, because as shown in Tables IV and V the same series contained the highest percentages of sucrose and of polysaccharides. Evidently there is a relationship between enzyme activity and chemical composition, but the exact nature of such a relationship is not yet apparent.

When the blades of the plants in the dark and the light (exclusive of the outdoor control) are compared, the following observation may be made. In the light, lack of water was associated with decreased invertase and sucrose, while in the dark, lack of water was associated with increased invertase and sucrose. Therefore it is not lack of water alone which is responsible for the differences, but some factor which develops differently in light and dark as a response to lack of water.

Enzyme Activity in Sheaths:

Table VII shows the greatest activity of invertase in series 5 only in the unbuffered tests. This may be explained by the hypothesis of Oparin (11), who suggests that McIlvaine's buffers tend to remove enzymes from the adsorbed condition and thus render their activity in different series more nearly equal. The sheaths thus differ from the blades, as in the latter the greatest invertase activity was found in series 5 in both the unbuffered and the buffered tests.

The buffered tests indicate a slight decrease in invertase activity in the dark, and also show that a period of seven hours in the light was sufficient for the invertase to become as active as in the outdoor control. Invertase activity in the sheaths was less severely affected by darkness than that in the blades.

Table VIII shows greater maltase activity in the sheaths of the plants supplied with water than in those deprived of water, in both the dark and the light. Intermediate activity was shown by the outdoor control.

Table IX shows that both amylase and dextrinase were very weak. No differences in activity were found in the different treatments.

Enzyme Activity in Green-Leaf Cane:

Table VII shows nearly equal invertase activity in all series when tested at pH 4.5, in the green-leaf cane. In the unbuffered tests the activity was weaker in series 1 (dark wet) than in the others, for which no explanation is now offered.

Although invertase activity was approximately equal in all the series, in the green-leaf cane, the sucrose content differed as shown in Table IV. Thus, although it is possible that differences in sucrose content may at times cause differences in invertase activity and vice versa, this is not an invariable occurrence. In the present instance the differences in sucrose content were probably due to differences in translocation rather than to immediate differences in enzyme action.

Table VIII shows that the activity of maltase was the greatest in series 4 (light dry), the others being equal. As recorded in Tables IV, V, and VI, series 4 was the highest in simple sugars and polysaccharides but the lowest in starch. Perhaps active maltase aids in speeding up the digestion of starch by hastening the removal of maltose, one of the end products of the digestion of starch. This would lead to a greater percentage of simple sugars, which might then be stored as polysaccharides other than starch.

Table IX shows that neither amylase nor dextrinase activity was detected in the green-leaf cane, but they may have been too weak for detection by our methods.

Enzyme Activity in Upper Dry-Leaf Cane:

Table VII shows that the activity of invertase was very weak in the upper dry-leaf cane. Series 4 (light dry) and 5 (outdoor control) were a little more active than the others, in the unbuffered tests. Differences in maltase activity due to treatment were minor, according to Table VIII. Neither amylase nor dextrinase was detected in the upper dry-leaf cane, according to Table IX. Thus the treatment in this experiment had little effect upon the activity of the enzymes tested in the upper dry-leaf cane.

Enzyme Activity in Lower Dry-Leaf Cane:

The activity of invertase in the lower dry-leaf cane was even weaker than in the upper, as shown in Table VII. So small were the differences that they can hardly be attributed to treatment.

In both the upper and lower dry-leaf cane, the plants deprived of water had the more sucrose, polysaccharides, and starch, as shown in Tables IV, V, and VI. Neither polysaccharides as a whole nor starch in particular can be translocated. Therefore they must be manufactured in place. Yet no amylase or dextrinase was detected according to Table IX. It is not possible to say that these carbohydrates were stored when the stem was young and contained more active enzymes, for then how would we explain the differences in carbohydrate content? The differences are recent and they occurred in place. Therefore either greater differences in enzyme action occurred in the living plant than were determined by our methods, or else starch may be synthesized in the presence of weak amylase and dextrinase when the conditions favor condensation (or union due to withdrawal of water).

The Effect of Water Upon Enzymes:

The effect of water upon the activity of the enzymes studied in this investigation is summarized in Table X, which shows that in the dark, water decreased the action of invertase and maltase but increased that of amylase and dextrinase in the blades. Water increased the activity of maltase in the sheaths. The enzymes in the other organs seemed not to be affected by the water supply, in the dark.

TABLE X

Effect of water upon enzymes.*

Organ	Invertase	Maltase	Amylase	Dextrinase
	in the dark			
Blades	—	—	+	+
Sheaths	0	+	0	0
Green-leaf cane	0	0	0	0
Upper dry-leaf cane	0	0	0	0
Lower dry-leaf cane	0	0	0	0
	in the light			
Blades	+	+	+	+
Sheaths	0	0	0	0
Green-leaf cane	0	—	0	0
Upper dry-leaf cane	0	—	0	0
Lower dry-leaf cane	0	0	0	0

* + = water increases action; — = water decreases action; 0 = no effect of water. (For invertase and maltase, differences less than 1 cc. N/20 $KMnO_4$.)

In the light, water increased the activity of the four enzymes studied in the blades. No other effect was shown except that water decreased the action of maltase in the green-leaf cane and in the upper dry-leaf cane.

Therefore the enzymes in the blades are more sensitive to differences in water supply than are those in the other organs of the plant. Further discussion of the effect of water upon enzyme activity and chemical composition will be postponed until the experiment has been repeated.

Summary

1. Certain aspects of the effect of water upon photosynthesis, translocation, storage of sugar, and enzyme activity were studied in sugar cane of the variety H 109.

2. Photosynthesis can take place in plants below the wilting point, as shown by increases in simple sugars and cane sugar in the blades of plants exposed to sunlight for seven hours after a period of 48 hours in absolute darkness.

3. Although photosynthesis can take place in plants below the wilting point, yet there is more photosynthesis in plants which are adequately supplied with water, as shown by their greater increases in simple sugars and cane sugar, and in addition by an increase in polysaccharides, under the conditions described in the preceding paragraph.

4. The translocation of carbohydrates takes place better in plants receiving an adequate supply of water than in plants below the wilting point.

5. Due to a curtailment in utilization, the storage of carbohydrates is greater in the plants deprived of water than in those supplied with water.

6. Although the plants deprived of water had the higher percentages of cane sugar in the tissue of the stem, the plants receiving water yielded in general the better juices, indicating that the sugar present in the plants receiving water was more readily expressed than that in the plants deprived of water.

7. A period of 48 hours of total darkness results in a decrease in the activity of invertase in the leaf-blades of the sugar cane plant.

8. The invertase in the blades is more responsive to changes in light and darkness when there is plenty of water than when the water supply is deficient.

9. The maltase in the blades is less sensitive to darkness than is invertase.

10. Withholding water resulted in an increase in the activity of invertase in the blades in the dark, but a decrease in the light. The activity of invertase in the other organs of the sugar cane plant seemed not to be affected by the water supply.

11. Withholding water resulted in a decrease in the activity of amylase and dextrinase in the blades.

12. The series of treated plants which had the most active invertase, amylase, and maltase in the blades was the series which had the highest percentages of sucrose and of polysaccharides in the blades.

13. The enzymes of the blades of the sugar cane plant (i. e., invertase, amylase, dextrinase, and maltase, the only ones studied) are sensitive to differences in moisture and light; the enzymes in the sheaths are less sensitive than those in the blades; the only enzyme in the green-leaf cane apparently affected by treatment was maltase; and in the dry-leaf cane any differences due to treatment were so small as to be insignificant.

Acknowledgments:

This experiment was undertaken in collaboration with Dr. Mangelsdorf and Mr. Wadsworth and the author takes pleasure in expressing her appreciation of their cooperation. Credit is due the Sugar Technology Department for conducting the juice analyses, and to Mr. Sa Ning for the darkening and the heating of the assembly room. Grateful appreciation is expressed in particular to Ada Forbes for her constant assistance during the experiment, and to Dr. Lyon for his valuable advice and helpful suggestions.

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Sugar Prices

96° CENTRIFUGALS FOR THE PERIOD
JULY 7, 1936, TO SEPTEMBER 3, 1936.

Date	Per Pound	Per Ton	Remarks
July 7, 1936	3.71¢	$74.20	Cubas.
" 8	3.70	74.00	Puerto Ricos.
" 28	3.65	73.00	Puerto Ricos.
Aug. 6	3.67	73.40	Philippines.
" 13	3.70	74.00	Puerto Ricos.
Sept. 3	3.65	73.00	Virgin Islands.

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